Graptolites from the Ontikan Limestones (Ordovician) of Öland, Sweden

II. *Graptoloidea and Graptovermida*

By

David Skevington

Abstract.—Descriptions are given of eighteen species and two subspecies of graptoloids and a possible graptovermid species from the Lower Ordovician Ontikan limestones of northern Öland.

One new graptoloid genus, *Aulograptus* gen. nov., is proposed and two other genera, *Holmograptus* Kozłowski and *Maeandrograptus* Moberg, are re-diagnosed. Two new species are described from Öland: one possibly belongs in *Maeandrograptus*, *M.* ? *geniculatus* sp. nov., and the other is attributed to *Pseudoclimacograptus* Přibyl, *P. camptochilus* sp. nov. The syntypes of *Tetragraptus bigsbyi* (Hall, 1865) are re-examined and shown to include two species. *Glyptograptus austrodentatus* var. *oelandicus* Bulman is elevated to the status of subspecies thereby becoming available in terms of the rules governing zoological nomenclature.

The taxonomic status of the family Corynoididae Ruedemann is discussed. It is considered probable that *Atopograptus* Harris and *Janograptus* Tullberg are invalid genera, having been founded on regenerated fragments of normal dichograptid rhabdosomes.

The level of the boundary between the graptolite Zones of *D. hirundo* and *D. bifidus* is concluded to lie between −118D and +23D at Hälludden and between −83 and D at Hagudden. In terms of the substage divisions of the Balto-Scandian Ordovician limestone sequence, the graptolite zonal boundary lies either at the Hunderum–Valaste junction or within the upper part of the Hunderum Substage.

Contents

Introduction

In Part I of the "Graptolites from the Ontikan limestones (Ordov.) of Öland, Sweden", material attributable to the orders Dendroidea, Tuboidea, Camaroidea and Stolonoidea was described. In addition, an introductory section gave details of the geography and stratigraphy of the localities of Hälludden and Hagudden, from which the graptolitic limestone was obtained, together with a description of the methods of preparation and illustration which were adopted; it is intended that this introduction shall serve also for Part II. In this second part, the description of the graptolites is completed with an account of the material referable to the order Graptoloidea and to Kozłowski's group of uncertain affinity, the Graptovermida; also, the conclusions reached concerning correlation are listed and discussed.

Indiscriminate usage of the term *stipe width* in the literature has caused the appended dimensions to have little value in specific descriptions, unless the statement is amplified in some way. In view of the lack of suitable alternatives, it is proposed to retain this term but to qualify it with appropriate adjectives. Thus, *lateral stipe width* refers to the distance between the two lateral walls of a stipe, seen in dorsal or ventral aspect, while *dorso-ventral stipe width* has reference to measurements made between the dorsal and ventral stipe margins.

In this latter case, it is necessary to indicate whether it is the *maximum* dorso-ventral width which is implied (from the dorsal margin to the distal tip of the ventral denticle, or to the ventral edge of the apertural margin of the theca if no denticle is developed), or the *minimum* dorso-ventral width, between the dorsal margin and the inner (or dorsal) edge of the thecal aperture.

The term *lappet* is used in a broader sense than is implied by the definition given in the Treatise (BULMAN, 1955, p. V6); thus, projections—be they expanded, pointed or rounded—developed on the lateral margins of thecal apertures, are so named.

The terms: *dicalycal theca*, *geniculum*, *infra-* and *supragenicular walls*, proposed and defined by JAANUSSON (1960, pp. 303–304), are used herein.

All figured specimens, with the exception of No. 485 (Fig. 67) from the HOLM Collection, and some additional material are housed in the Museum of the Palaeontological Institute, University of Uppsala, Sweden, and are numbered Öl. 1165–Öl. 1240.

I would again like to acknowledge the help given me by those persons whose names are listed in Part I (p. 3); in addition, Dr. ROLAND SKOGLUND (Uppsala) is thanked for his assistance in the identification of certain graptoloid species, and it is with great pleasure that I again record my indebtedness to Dr. VALDAR JAANUSSON (Uppsala) for his interest and help in the preparation of this paper and for undertaking the task of guiding it through the press.

A visit to Sweden was made possible by a grant from the British Council, to whom I offer my sincere thanks, and I would like also to express my gratitude to Professor PER THORSLUND (Uppsala) and Professor GERHARD REGNÉLL (Lund) for their help and kindness during my stay in Sweden.

Systematic Description

Order Graptoloidea LAPWORTH, 1875

Family Dichograptidae LAPWORTH, 1873

Genus *Tetragraptus* SALTER, 1863

DISCUSSION.—The genus *Tetragraptus* is represented, in the Ontikan limestones of Öland, by numerous fragmentary remains derived from the lower levels of the cliff sections at both Hälludden and Hagudden. No complete rhabdosome has been recovered; in the better preserved specimens, one or, perhaps, two main stipes—or parts thereof—remain attached to a proximal end; most commonly, however, only proximal ends with the main stipes severed at the base, or fragments of main stipes, have been forthcoming. Since the several species of *Tetragraptus* are defined largely according to the attitude of their main stipes, the identity of much of the Ontikan limestone tetragraptid material must necessarily remain in doubt.

One species, however, is clearly defined: *Tetragraptus bigsbyi* (HALL, 1865), recovered from the lowest levels from which collections were made at Hälludden and Hagudden (−84 −92 and −83 −86, respectively). The name

Graptolithus bigsbyi was given by HALL (1865) to specimens which he had earlier (1858) incorrectly described in *Phyllograptus*, as *P. similis*; the change of specific name was necessary because, in 1865, *Graptolithus similis* (now *Didymograptus similis*) was occupied. The currently valid name for HALL's reclined tetragraptid is *Tetragraptus bigsbyi* (HALL, 1865); *similis*, 1858, having been replaced by *bigsbyi*, 1865, cannot now be revived (see BERRY, 1960, p. 53).

In renaming *Phyllograptus similis* as *Graptolithus bigsbyi*, HALL clearly had in mind only a change of name to avoid homonymy, but, at the same time, he inadvertently extended the species: thus, *P. similis*, as originally defined (1858), includes the specimens figured by HALL (1865) as pl. 16, figs. 25, 26, 29 and 30—but not the form represented by figs. 22–24, 27 and 28, which he also incorporated in *G. bigsbyi*. The originals of the latter group of figures differ in possessing a less scandent rhabdosome, less strongly overlapping thecae with more prominent denticles, and generally straight, parallel-sided main stipes. The name *Tetragraptus bigsbyi* (HALL, 1865) must be reserved for the material first described as *Phyllograptus similis*. For the additional material included within *Graptolithus bigsbyi* by HALL (1865), an existing valid name, if one can be found, would suffice; otherwise, a new name must be proposed. The writer does not know of any available valid name which could be used; consequently, this additional material is given a new name, *Tetragraptus pseudobigsbyi*, which has been chosen with the intention of indicating something of the history of the species.

The tetragraptid material recovered, other than that attributed to *T. bigsbyi* (HALL), includes about six proximal end specimens in which a sufficient length of second order stipe is preserved to enable the form of the complete rhabdosome to be deduced. In some instances, the main stipes lie scarcely above the horizontal; in others, they may be described as exhibiting moderate inclination; and in the remainder, the stipes are near-scandent—yet, the proximal ends, so far as can be judged from external evidence, portray an identical stage of development in every case. This latter has been fully described and illustrated by HOLM (1895) and BULMAN (1936), in material which they attribute to *T. bigsbyi* (HALL); the affinities of the material of these authors is commented upon below.

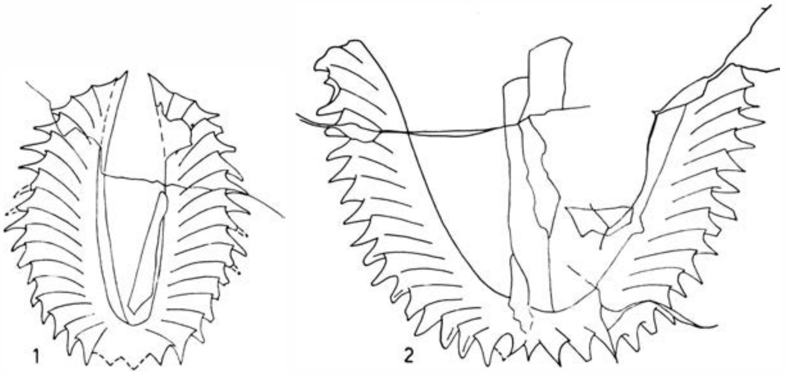
Complementary to the problem of the proximal end of the rhabdosome is that concerning the affinity of isolated fragments of second order stipes which give no indication of their original attitude, whilst the variation occurring in stipe width and thecal number within a single species further complicates the issue.

Tetragraptus bigsbyi (HALL, 1865)

Figs. 1, 3, 5, 6

1865 *Graptolithus bigsbyi* n.sp.—HALL, pl. 16, figs. 25, 26, 29, 30 [*non* figs. 22–24, 27, 28 = *Tetragraptus pseudobigsbyi* n.sp.].

1858 *Phyllograptus similis* n.sp.—HALL, p. 140.



Figs. 1–2: (1) *Tetragraptus bigsbyi* (Hall, 1865). Lectotype. × 3.3. Point Levis, Quebec (? Levis zone C3); Geol. Survey Canada No. 923*a*. (2) *Tetragraptus pseudobigsbyi* sp. nov. Holotype × 3.6. Point Levis, Quebec (? Levis zone C3); Geol. Survey Canada No. 923*b*.

1902 *Tetragraptus bigsbyi* (Hall)—Elles & Wood, p. 68, pl. VI, figs. 6*d*, *e*.
1904 *Tetragraptus similis* (Hall)—Ruedemann, pl. 12, ? fig. 6; p. 660, ? text fig. 60.
1947 *Tetragraptus similis* (Hall)—Ruedemann, pl. 51, fig. 4 (from Hall, 1865), ? fig. 11.
1955 *Tetragraptus bigsbyi* (Hall)—Bulman, p. V58, fig. 39.
1958 *Tetragraptus similis* (Hall)—Rigby, pl. 118, ? fig. 13.
1960 *Tetragraptus bigsbyi* (Hall)—Berry, pl. 7, fig. 11.

Lectotype.—No. 923*a*, Geol. Surv. Canada Coll.; pl. 16, fig. 30 in Hall (1865) and refigured herein as Fig. 1.

Type locality and Horizon.—Pt. Levis, Quebec; possibly from Levis, zone C3.

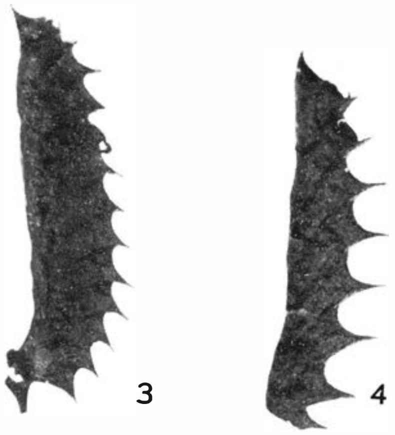
Description of Lectotype.—Rhabdosome ovate and short, approximately 10 mm in length. The second order stipes are highly reclined or near-scandent; the distal tips may converge. The dorsal margin is straight, or shows slight concave curvature with a consequent increase in inclination distally. In the left-hand stipe (Fig. 1), the greatest dorso-ventral stipe width (including the apertural denticle) is 3.1 mm, and is achieved at the ninth theca; from this theca, stipe width decreases to the proximal and distal ends of the stipe.

The thecae are curved throughout their length, with the angle of inclination to the dorsal wall progressively increasing from thecal origin to aperture. The apertural margin is straight or slightly concave, and is provided with a broad, swept-back denticle lying in the plane of the aperture. Overlap ranges from 0.75–0.80 and the free ventral wall is largely comprised of the ventral denticle; 13–14 thecae are developed per cm.

Figured Material from Öland.—Nos. Öl. 1165–Öl. 1167.

Locality and Horizon of Material from Öland.—Hälludden: −84 −92; Hagudden: −83 −86.

Description of the Material from Öland.—The sicula averages 2.1 mm



Figs. 3–4: (3) *Tetragraptus bigsbyi* (HALL, 1865). Complete second order stipe. × 5. Hagudden −83 −86; Öl. 1166. (4) *Tetragraptus* cf. *T. pseudobigsbyi* sp. nov. Incomplete, slender, second order stipe. ×7.5. Hälludden −118 −120D; Öl. 1178.

in length, from the base of the nema to the aperture; a broad, roundly-terminated denticle, up to 0.4 mm long, is developed ventrally on the apertural margin. The width of the aperture ranges from 0.45–0.62 mm reflecting variable compression of the sicula. Though straight for the greater part of its length, the sicula is curved slightly towards the anti-'virgellar' side as the aperture is approached.

The first two thecae, where they leave the sicula, enclose an angle of 110°–120°. They do not diverge symmetrically, however, and the angle contained within the walls of the sicula and th1^1 is a right angle.

The second order stipes average 1.0 mm in dorso-ventral width at origin; the greatest width in each stipe is gradually achieved and is not usually maintained for more than two or three thecae. This may be illustrated as follows:

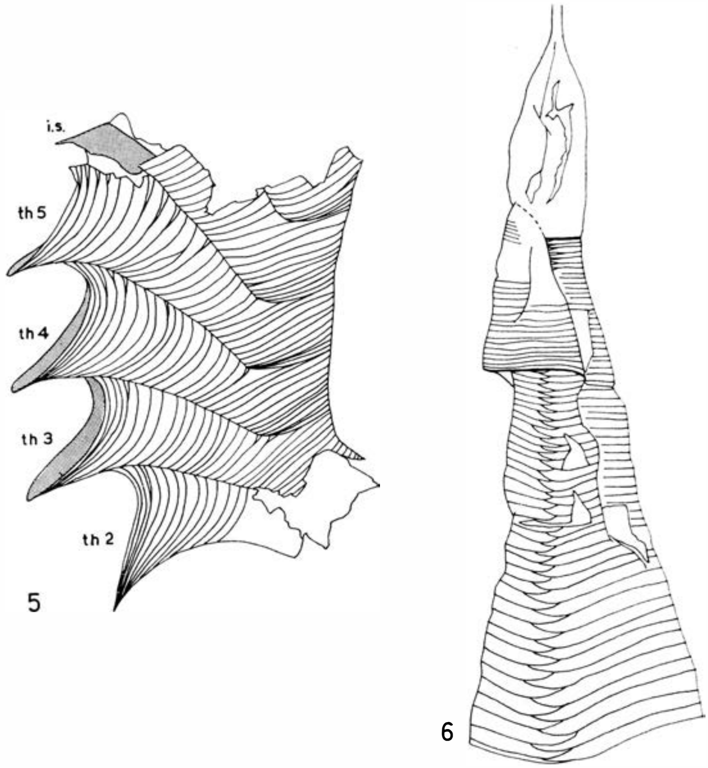
Spec. No. Öl. 1167 (Fig. 3); a second order stipe (^{1}a).

Thecal No.	2^1a	3^1a	4^1a	5^1a	6^1a	7^1a	8^1a	9^1a
d.-v. width (incl. denticle) in mm.	2.0	2.25	2.25	2.4	2.5	2.6	2.6	2.5

Spec. No. Öl. 1168; a main stipe of unknown position in the rhabdosome.

Thecal No.	2	3	4	5	6	7	8	9
d.-v. width (incl. denticle) in mm.	—	2.2	2.5	2.6	3.0	3.2	3.4	3.5

The only complete second order stipe (Öl. 1167, Fig. 3) has a greatest width of only 2.6 mm; Öl. 1168, however, indicates that greater widths are possible in this species. The length of stipe ^{1}a in Öl. 1167 is 10 mm, which is normal for the species, and increased width of stipe does not necessarily imply greater length (cf. HALL, 1865, pl. 16, figs. 25 and 29). The dorsal stipe wall is generally straight, or it may show slight concave curvature so that inclination to the median axis of the rhabdosome increases distally.



Figs. 5–6: *Tetragraptus bigsbyi* (HALL, 1865). (5) Proximal fragment of second order stipe. × 17. Hagudden −83 −86; Öl. 1165. (6) Immature sicula with initial bud. × 75. Hagudden −83 −86; Öl. 1167. *i.s.*: interthecal septum; *th*: theca.

The thecae are characteristically curved throughout their length (Fig. 5); the angle between the dorsal stipe margin and the trace of the interthecal septum increases as the thecal aperture is approached, to such an extent that the more proximal thecae may be recurved. Proximally, thecal overlap is about 0.75; distally, it may be as great as 0.82.

The plane of the apertural margin is straight, or slightly concave, and the ventral denticle is swept back to such a degree that it lies almost in this plane. The thecae increase in width progressively towards their apertures, which, in the mature part of the stipe, have a dorso-ventral dimension of 1.0 mm.

In Öl. 1167 (Fig. 3), 12 thecae are developed in the 10 mm of stipe.

THE INTERTHECAL SEPTUM.—In the advanced proximal end growth stage of *Tetragraptus bigsbyi* figured by BULMAN (1955, p. V58, fig. 39.1), the dorsal wall of th2^2a is in advance of the growing edge of th3^2a, and the interthecal septum, at this stage, is clearly the dorsal wall of the parent theca. In Öl. 1165 (Fig. 5), however, the ventral wall of the daughter theca is seen to extend beyond the aperture of the parent theca—this indicates that, whilst the initial portion of the septum is composed of growth bands which are continuous with those of the parent theca, the distal portion is formed by the daughter theca.

The first 0.5 mm or so of the interthecal septum is flat, but, thereafter, it gradually assumes a downwardly convex form, consistent with it being the ventral wall of the daughter theca. The change in the form of the septum may correspond with the change in the mode of its formation, and since the former is gradually achieved, the latter may take place by the progressive intercalation of fuselli, ultimately leading to the replacement of those continuous with the dorsal wall of the parent theca by those from the ventral wall of the daughter theca.

DEVELOPMENT.—The prosicula increases gradually in width from the base of the nema to the distal margin (Fig. 6), and is from 0.30–0.35 mm in length. Only occasional longitudinal rods are discernible in those specimens showing the prosicula.

The metasicula (Fig. 6) expands gradually to the aperture. The growth bands on the ventral side sweep downwards to an increasing degree as the aperture is approached, giving rise to a prominent denticle. This latter is roundly-terminated and has sub-parallel sides; the final few growth bands may be pinched out, laterally.

The initial bud develops from the prosicula (Fig. 6), on the ventral side, 0.20–0.25 mm below the base of the nema. Growth is downwards, parallel to the wall of the sicula; th1^2 originates 0.82–0.88 mm below the initial foramen—that is, about half-way between this latter and the sicula aperture (see BULMAN, 1955, fig. 39.1). Th1^1 continues the downward direction of growth of the initial bud to just short of the sicula aperture, where it diverges from the ventral wall of the sicula at an angle approaching 90°; this angle is quickly reduced, however, by concave curvature of the ventral wall of the theca.

Th1^2 grows obliquely across the sicula, and leaves this latter at the level of the aperture, on the dorsal side. In *T. bigsbyi*, th1^2 is dicaycal. Th2^1 arises quickly and is directed horizontally across the sicula onto the dorsal wall of th1^1; th2^2 is produced from th1^2 but at a lower level, and on the opposite side to th2^1.

The first four thecae of the second order stipes —1^1*a*, *b* and 2^2*a*, *b*—originate within 0.6 mm of the appearance of th2^1 and th2^2, respectively.

***Tetragraptus pseudobigsbyi* sp. nov.**

Fig. 2

1865 *Graptolithus bigsbyi* n.sp.—HALL, pl. 16, figs. 22–24, 27, 28 [*non* figs. 25, 26, 29, 30 = *Tetragraptus bigsbyi* (HALL)].

HOLOTYPE.—No. 923*b*, Geol. Surv. Canada Coll., pl. 16, fig. 23 in HALL (1865) and refigured herein as Fig. 2.

TYPE LOCALITY AND HORIZON.—Pt. Levis, Quebec; possibly from Levis, zone C3.

DESCRIPTION OF HOLOTYPE.—The second order stipes are highly reclined and straight, or slightly flexed and more concave proximally and more convex distally. In the right-hand stipe, a uniform dorso-ventral width of 2.9 mm (including the apertural denticles) is achieved at the level of the fifth theca; in the left-hand stipe the uniform width is 3.2 mm, and the difference can probably be accounted for by distortion. The preserved length of the left-hand stipe in Fig. 2 is 11 mm.

The thecae are straight for much of their length, and inclined at 45°–55° to the dorsal wall; as the aperture is approached the inclination increases. Overlap is of the order of 0.65; 12–13 thecae are developed per cm. The apertural margin is strongly concave, while the prominent apertural denticle follows the curvature of the free ventral wall and is not appreciably swept back.

***Tetragraptus* cf. *T. pseudobigsbyi* sp. nov.**

Fig. 4

1895 *Tetragraptus bigsbyi* (HALL)—HOLM, p. 340, text figs. 1–6, pl. 11, figs. 9–16; ?pl. 12, figs. 1–3, pl. 13, figs. 13–16.

1936 *Tetragraptus bigsbyi* (HALL)—BULMAN, p. 30, text figs 8–12, pl. 4, figs. 11, 12; ?pl. 1, figs. 16–20, 22, 23.

FIGURED MATERIAL.—No. Öl. 1178.

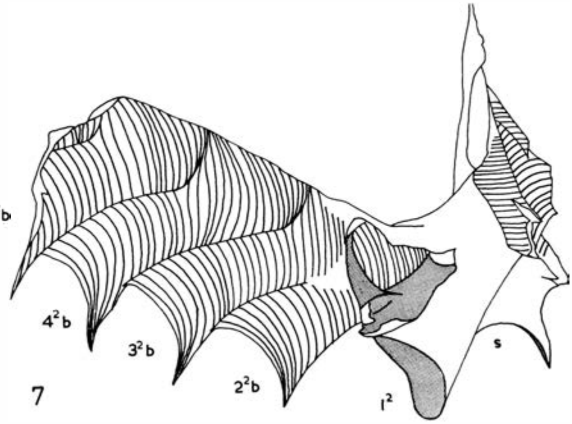
LOCALITY AND HORIZON.—Hälludden: −118−120D.

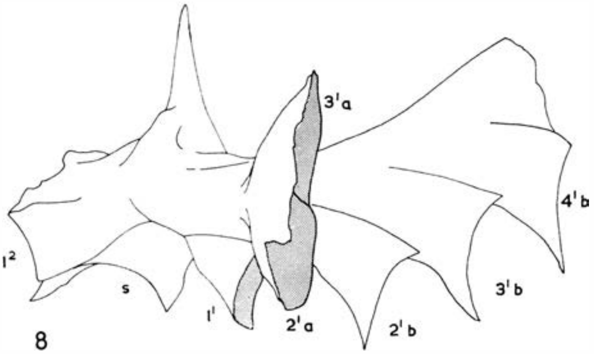
DESCRIPTION.—Those fragments of the proximal end in which the bases, at least, of the second order stipes are preserved, show that these latter adopted a near-scandent attitude in the complete rhabdosome. Apart from this feature, however, such proximal ends are indistinguishable from those of *Tetragraptus* cf. *T. reclinatus* and *T.* cf. *T. serra.*

Isolated fragments compared with *T. pseudobigsbyi* are those lengths of second order stipes in which the dorsal wall is concavely curved, indicating the development of a more scandent attitude distally.

Dorso-ventral stipe width, including the apertural denticles, is of the order of 2.0–2.1 mm, though one specimen (Fig. 4) does not exceed 1.65 mm. Thecal length averages 2.0 mm; overlap is 0.6; and 12–13 thecae are developed per cm. The thecae are typically slightly curved throughout their length, with inclination to the dorsal wall increasing as the aperture is approached; the apertural margin is concave, and the prominent denticles continue the line of curvature of the free ventral wall.

DISCUSSION.—Comparison with *T. pseudobigsbyi* is based on the evidence of scandency provided by the proximal end specimens, together with the presence of more thecae per cm than in *T.* cf. *T. serra.* Specimen Öl. 1178 (Fig. 4) may be compared with some of HOLM's (1895) material, the main stipes of which can be extremely slender; the form described as *T. bigsbyi* var. *askerensis* by MONSEN (1937) also appears to be similar.





Figs. 7–8: *Tetragraptus* cf. *T. reclinatus* Elles & Wood, 1902. (7) Damaged proximal end in reverse aspect. × 18. Hälludden −118−120D; Öl. 1170. (8) Damaged proximal end in reverse aspect; note low inclination of second order stipes. × 17. Hälludden −118−120D, Öl. 1171*a*. *s:* sicula.

***Tetragraptus* cf. *T. reclinatus* Elles & Wood, 1902**

Figs. 7, 8

cf. 1902 *Tetragraptus reclinatus* n.sp.—Elles & Wood, p. 67, text fig. 41, pl. VI, figs. 5*a–e*.

1936 *Tetragraptus bigsbyi* (Hall)—Bulman, pl. 1, fig. 21.

Figured Material.—Nos. Öl. 1170, Öl. 1171*a*.

Locality and Horizon.—Hälludden: −135−140D, −118−120D.

Description.—The sicula, including the apertural denticle, is from 2.1–2.7 mm in length; the denticle itself ranges from a slight protuberance to a prominent, roundly-terminated process, 0.4 mm long. The diameter of the sicula aperture varies from 0.58–0.65 mm.

The main stipes are initially inclined at an angle above the horizontal not exceeding 35° (Figs. 7, 8) and which is frequently appreciably less than this. The dorsal margin is convexly curved, so that the stipes approach the horizontal distally. The longest fragment of second order stipe recovered is 16.5 mm in length. The main stipes are narrow at their origin, averaging 0.62 mm, but the dorso-ventral width increases rapidly to the level of the third or fourth theca of the stipe and then remains uniform within the range 1.65–1.98 mm; however, the majority of the main stipe fragments recovered are between 1.70 and 1.75 mm in width.

Proximally, the thecae are inclined at a high angle to the dorsal margin and 14–15 thecae may be developed per cm; overlap is of the order of 0.75. The distal thecae are inclined at about 40° to the dorsal wall, though steepening aperturally; only 12–13 occur per cm and overlap is within the range 0.50–0.65. The length of a distal theca is 1.7–1.9 mm and the apertural diameter 0.6 mm.

The thecae are strongly denticulate; the denticles may follow the course of the interthecal septa, or may be slightly swept back (though never to the extent seen in *T. bigsbyi*). The apertural margin, in lateral aspect, is distinctly concave.

Characters of specific significance include the slender, reflexed form of the main stipes, combined with an initial low angle of inclination above the horizontal.

DISCUSSION.—The Öland material differs from *T. reclinatus* in having narrower stipes and a longer sicula; furthermore, the stipes are reflexed rather than reclined. However, *T. reclinatus* is the only described species of *Tetragraptus* having slender stipes set obliquely above the horizontal—for this reason, the present material is compared with that species.

Tetragraptus cf. *T. serra* (BRONGNIART, 1828)

Figs. 9, 10

cf. 1828 *Fucoides serra* n.sp.—BRONGNIART, p. 71, pl. vi, figs. 7, 8.

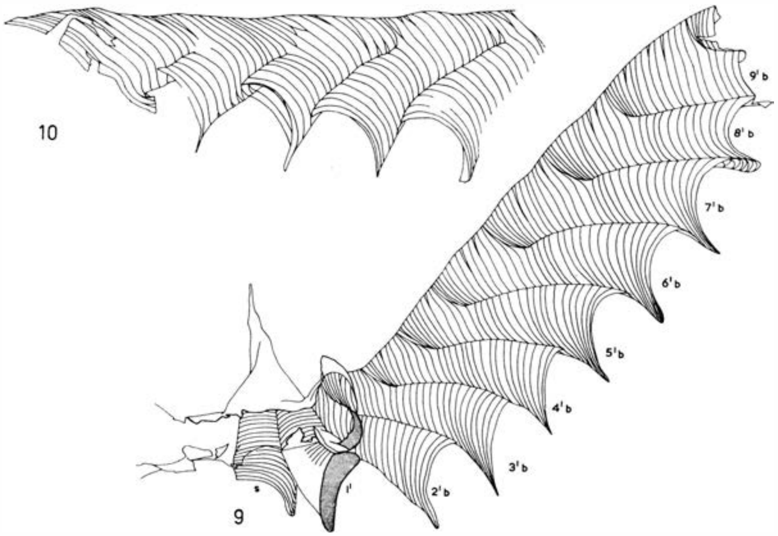
cf. 1902 *Tetragraptus serra* (BRONGNIART)—ELLES & WOOD, p. 65, text fig. 40, pl. VI, figs. 4*a–f*.

1936 *Tetragraptus bigsbyi* (HALL)—BULMAN, pl. I, fig. 15.

FIGURED MATERIAL.—Nos. Öl. 1174, Öl. 1175.

LOCALITY AND HORIZON.—Hälludden: −118−120D.

DESCRIPTION.—Specimen Öl. 1174 (Fig. 9) includes the proximal end of the rhabdosome and the whole of stipe ^{1}b, apart from the growing tip. The sicula, with the apertural denticle, is 2.4 mm in length; the denticle itself is 0.4 mm long. The initial bud appears 0.30 mm below the base if the nema, and th1^2 is produced 0.4 mm below this. Stipe ^{1}b is 6.0 mm in length; the dorsal margin is straight apart from the distal tip, which is curved away from the axis of the rhabdosome; the stipe is inclined at 60° above the horizontal. The dorso-ventral width of the stipe is 1.0 mm at origin, increasing to 2.0 mm at th2^{1}b (including the apertural denticle) and to 2.3 mm at th6^{1}b. The latter theca is 2.1 mm in ventral wall length and 0.82 mm wide at the aperture; 0.75 of the theca is overlapped. The thecae in stipe ^{1}b are inclined at 40° to the dorsal margin, though this angle increases as the aperture is approached; the apertural



Figs. 9–10: *Tetragraptus* cf. *T. serra* (Brongniart, 1828). (9) Proximal end in reverse aspect; note moderate inclination of second order stipe. × 17. Hälludden − 118 − 120D; Öl. 1174. (10) Growing end of a second order stipe. × 11. Hälludden − 118 − 120D; Öl. 1175. *s:* sicula.

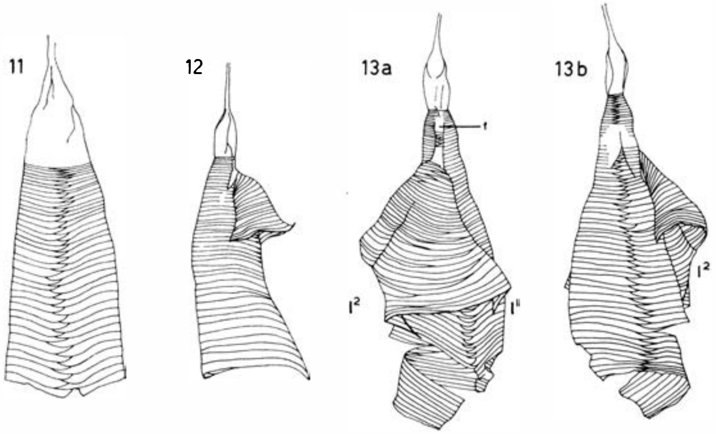
denticle follows the curvature of the ventral wall. Five thecae are present in 4.3 mm, suggesting 11–12 per cm proximally.

The remaining material is largely fragmentary, but affords some indication of the range of variation to be expected. The stipes are of uniform dorso-ventral width, except proximally and distally; the width at origin is not less than 0.75 mm, increasing to 2.0–2.8 mm (with the apertural denticle) at the level of the fourth or fifth theca of the stipe. Proximally, 10–12 thecae per cm are developed and overlap is of the order of 0.75–0.79. Distally, the thecae number only 8–10 per cm and overlap is reduced to about 0.65.

The distinguishing features of the material are the attitude of the stipes (when this can be determined), and the relatively few thecae per cm developed distally.

The Interthecal Septum.—This appears to be formed entirely by the ventral wall of the younger of two adjacent thecae. Thus, in Öl. 1175 (Fig. 10), the growth lines of the lateral walls of one theca can be traced into those of the interthecal septum separating this theca from the preceding one. Furthermore, throughout the length of the septum, there is no evidence of the intercalation of fuselli which might suggest a change in the formation of the septum from the ventral wall of the daughter theca to the dorsal wall of the parent theca. The septum is convexly arched proximally from its origin to the beginning of the free ventral wall, which is consistent with it being the ventral wall of the younger of two adjacent thecae throughout the whole of its length.

Discussion.—The material differs from *T. serra* (Brong.) in possessing a



Figs. 11–13: *Tetragraptus* sp. indet. (11) Immature sicula. ×42. Hälludden −118−120D; Öl. 1179. (12) Immature sicula with initial bud. ×24. Hälludden −118−120D; Öl. 1180. (13) Damaged sicula with initial bud and origins of th 1^1 and th 1^2; (13*a*) reverse aspect; (13*b*) obverse aspect. ×24. Hälludden −118−120D; Öl. 1181. *f:* initial bud; *s:* sicula.

greater number of thecae per cm and in having narrower stipes, though in this latter respect it should be noted that Elles & Wood (1902) record a slender form of *T. serra*, for which, however, a name has not been proposed.

T. serra Monsen (1937) may be conspecific with the present material, but the state of preservation of the former is such that a decision cannot be reached.

Early Developmental Stages.—Early stages in the mode of proximal end development described by Bulman (1936, pp. 33–39) have been recovered and cleared (Figs. 11, 12, 13*a–b*).

The prosiculae are usually either too badly preserved or else insufficiently cleared to reveal anything of the structure, except for the presence of occasional longitudinal rods, though, in one instance, five coils of the helicoidal thread have been observed.

In the earliest growth stages of the metasicula, before the downward deflection of fuselli on the ventral side is initiated (denoting the presence of a ventral denticle), the growing edge is straight and orientation would be impossible but for the fact that the zig-zag suture on what is later determined as the ventral side is quite regular (Fig. 11), whilst the corresponding dorsal suture is markedly irregular. At a later stage, however, the latter suture becomes increasingly better developed, and a very slight denticle is ultimately produced on the dorsal margin of the sicula aperture. The ventral denticle is triangular in outline—broad at the base but narrowing terminally; lateral pinching out of fuselli has not been observed.

The growth of the sicula is not completed, at least, until the appearance of th 1^2 (Figs. 13*a*, *b*), and possibly not until a much later stage in development.

The initial bud is produced in a resorption foramen on the ventral side of the metasicula, close to the distal margin of the prosicula: the top of the foramen is only 0.07 mm below this margin in Öl. 1180 (Fig. 12). The initial bud grows down the sicula, expanding rapidly in the process, and within 0.4 mm of its appearance it gives rise to the foramen of th1^2 (Fig. 12).

The proximal ends of mature rhabdosomes (see Figs. 7, 8, 9) show that th1^1 continues the downward direction of growth of the initial bud to about the level of the sicula aperture, where it diverges at an angle of 55°–60° from the ventral wall of the sicula. Th1^2 grows obliquely across the sicula, leaving it at the dorsal margin of the aperture. Th2^1 and th2^2 are produced from the dicalycal theca th1^2, shortly after its appearance, and at the same level, but on opposite sides of the theca. These two thecae subsequently divide to give the first four thecae of the second order stipes.

Discussion of the Öland Tetragraptids

On the basis of mode of development of the proximal end, *T. bigsbyi* (HALL) is readily separable from the other tetragraptids recovered from the Ontikan limestones of Öland, which have been provisionally identified as *T.* cf. *T. reclinatus*, *T.* cf. *T. serra* and *T.* cf. *T. pseudobigsbyi*.

In this latter group, the distinctions between species have been based, to a large extent, on the attitude of the second order stipes to the median axis of the rhabdosome, and to a much lesser degree on stipe dimensions and thecal abundance. It has not been found possible, however, on the basis of mode of development, to distinguish between those proximal end specimens to which are attached near-scandent stipes (*T.* cf. *T. pseudobigsbyi*), those with moderately inclined stipes (*T.* cf. *T. serra*), and those with stipes inclined only slightly above the horizontal (*T.* cf. *T. reclinatus*).

Species of *Tetragraptus* are at present defined primarily on the basis of stipe attitude but not at all according to mode of development, and, as shown, stipe attitude and dimensions may vary whilst the stage of development remains constant. Thus, the study of isolated, as against shale-preserved, material increasingly demands a revision of taxonomic values.

Using development as a basis of classification, one may identify two 'species' amongst the Öland tetragraptids:

'*Species*' *1:* the initial bud arises in the prosicula; th1^2 is produced almost 1.0 mm below the point of appearance of the bud; the origins of the first three thecae accord with the *gibberulus* stage of the isograptid type of development —*T. bigsbyi.*

'*Species*' *2:* the initial bud is produced in the metasicula and gives rise to th1^2 within 0.5 mm of its appearance; the origins of the proximal thecae comply with the requirements of the *hirundo* stage of the isograptid type of development —*T.* cf. *T. reclinatus*, *T.* cf. *T. serra* and *T. pseudobigsbyi.*

The observed variations in stipe attitude and dimensions may perhaps be of value as bases for the subdivision of these 'species'.

Such a classification of the Öland tetragraptids may prove useful from a stratigraphical point of view: *T. bigsbyi* is recorded only from the lowest levels at Hälludden and Hagudden from which collections were made (−84−92 and −83−86, resp.); the members of the second group are confined to the −135−140D and −118−120D levels at Hälludden—none have been recovered from limestones from the Hagudden section.

Genus *Phyllograptus* HALL, 1858

Phyllograptus angustifolius HALL, 1858

Figs. 14–16

1858 *Phyllograptus angustifolius* n.sp.—HALL, p. 139.
1895 *Phyllograptus angustifolius* HALL—HOLM, p. 345, pl. 13, figs. 1–12, pls. 14–16.
1936 *Phyllograptus angustifolius* HALL—BULMAN, p. 39, text figs. 13–16, pl. 1, fig. 26, pl. 4, figs. 7–10.
1947 *Phyllograptus angustifolius* HALL—RUEDEMANN, p. 315, pl. 53, figs. 2–6, (with full synonymy).

FIGURED MATERIAL.—Nos. Öl. 1182, Öl. 1183*b*, Öl. 1184.

LOCALITY AND HORIZON.—Hälludden: −113−116D, −110−113D, −100D.

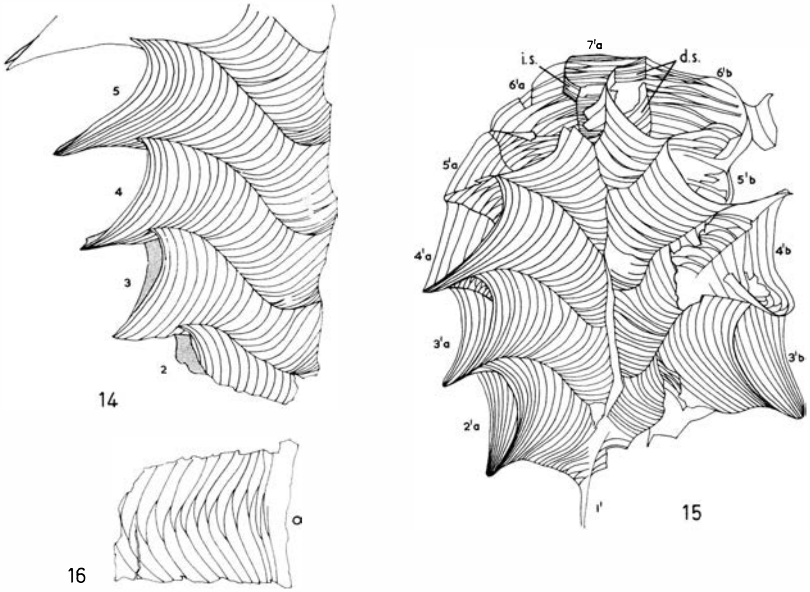
DESCRIPTION.—The recovered specimens are of interest only in that some have responded to treatment in SCHULZE's solution, allowing growth lines to be traced and internal structures to be identified; for a full description of this species, attention is directed particularly to the works of HOLM (1895) and BULMAN (1936).

No attempt has been made to isolate several large fragments of rhabdosome. The largest of these is 14.7 mm long and has a greatest width of 5.8 mm, with a distinct decrease to each extremity, suggesting that the complete specimen did not greatly exceed the preserved length.

The isolated material includes a near-proximal fragment of rhabdosome, a portion of which is reproduced as Fig. 14. The greatest rhabdosomal width in this specimen, including the apertural denticles, is 5.82 mm. Growth lines are readily evident; at the origin of each theca, a marked 'unconformity' is developed in the growth lines, and is attributable to the pronounced curvature of the proximal thecae. Distally in the rhabdosome, where curvature of the thecae is reduced, only slight irregularity results at thecal origins.

In the cleared growing end specimen, Öl. 1183*b* (Fig. 15), two stipes are preserved, growing independently of each other. The slightly sinuous dorsal septum, the interthecal septa, and the points of origin of the thecae, are all clearly illustrated.

THE INTERTHECAL SEPTUM.—The interthecal septum in *P. angustifolius* is a single unit, as in *Tetragraptus* cf. *T. serra*. Evidence for this is provided by an isolated and cleared septum (Fig. 16) in which the growth lines remain quite regular throughout its length, although they cannot be deciphered at the



Figs. 14–16: *Phyllograptus angustifolius* HALL, 1858. (14) Proximal end of a single stipe. × 17. Hälludden −110−113D; Öl. 1182. (15) Damaged proximal end growth stage; view is into the angle between stipes 1_a and 1_b. × 17. Hälludden −110−113D; Öl. 1183*b*. (16) Isolated interthecal septum, cleared except for thickened proximal margin. × 24. Hälludden −113−116D; Öl. 1184. *d.s.*: dorsal septum; *i.s.*: interthecal septum; *o*: proximal margin of interthecal septum.

thickened proximal margin. Nowhere is there a suggestion of the intercalation of fuselli, or of a change over from those of one theca to those of the succeeding or of the preceding theca.

If the above observations are valid, then the interthecal septum between two adjacent thecae, th'n' and th'n + 1', must be composed, in its entirety, either of the dorsal wall of th'n' or of the ventral wall of th'n + 1'; the fact that the apertural continuation of the septum (i.e. the free ventral wall) is the ventral wall of th'n + 1', indicates the latter to be the correct alternative.

***Phyllograptus angustifolius* cf. *elongatus* BULMAN, 1931**

cf. 1931 *Phyllograptus angustifolius* var. *elongatus* n.var.—BULMAN, p. 46, pl. 3, figs. 1, 2.
cf. 1937 *Phyllograptus angustifolius* var. *elongatus* BULMAN—MONSEN, p. 212, pl. 19, figs. 1–3.

LOCALITY AND HORIZON.—Hälludden: −113−116D.

DESCRIPTION.—In the single specimen recovered the total preserved length of the rhabdosome is 28 mm, and the greatest width, of 4 mm, is achieved within 1 cm of the proximal end; the rhabdosome, apart from tapering proximally, is parallel-sided. 12 thecae are developed in the first cm; slightly fewer are present distally, where the inclination of the thecae to the dorsal septum is less.

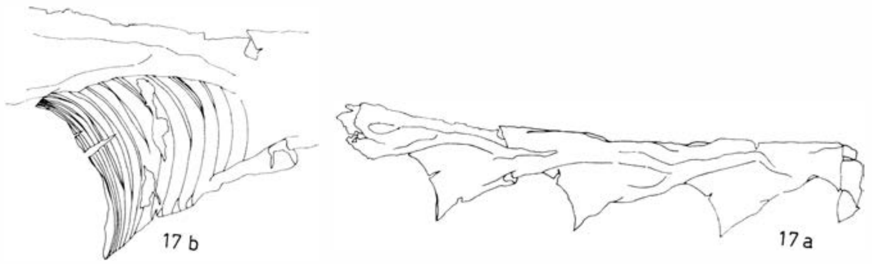


Fig. 17: *Didymograptus formosus* Bulman, 1936. (17) Fragment of stipe, (17*a*) complete specimen, × 18; (17*b*) part of latter enlarged to show growth lines in vicinity of thecal aperture, × 44. Hälludden − 118 − 120 D; Öl. 1188.

Discussion.—The slender, parallel-sided form of the rhabdosome, with an observed minimum length of almost 3 cm, favours the inclusion of this specimen (Öl. 1187) in Bulman's variety of *P. angustifolius*, but the uncertain maximum length and the presence of slightly too many thecae per cm proximally (12, as compared with a quoted range for var. *elongatus* of 9–11), suggests that such an identity should be provisional.

Remarks.—The single specimen recovered is preserved in a fragment of limestone. An attempt was made to clear the proximal end, which was separated and isolated for the purpose, but the coating of pyrite and secondary thickening successfully resisted all efforts to achieve this end.

Genus *Didymograptus* M'Coy, 1851

Didymograptus formosus Bulman, 1936

Figs. 17–23

1936 *Didymograptus formosus* n.sp.—Bulman, pp. 24–26, pl. 1, figs. 5–7, text fig. 6.
1954 *Didymograptus formosus* Bulman—Kozłowski, pp. 424, 426 (footnote).
1960 *Didymograptus formosus* Bulman—Jaanusson, p. 341, Table 8.

Figured Material.—Nos. Öl. 1188, Öl. 1189 a, b, Öl. 1190–Öl. 1193.

Locality and Horizon.—Hälludden: − 135 − 140 D, − 118 − 120 D, − 113 − 116 D; Hagudden: 0–8 D.

Diagnosis (amended).—Rhabdosome small, declined or deflexed; angle of divergence of stipes at sicula from 90°–150°. Dorso-ventral stipe width up to 0.75 mm at thecal apertures; 11–14 thecae per cm; overlap 0.33–0.5. Sicula slender, typically 1.0–1.2 mm in length; apertural width 0.3–0.4 mm; slightly curved distally; provided with prominent virgella. Development: *extensus* stage of isograptid type.

Description.—This species was described by Bulman (1936) from uncleared, dry-mounted material in the Holm Collection. The present specimens, which include several growth stages, have readily cleared, providing details of the early developmental stages of the species.

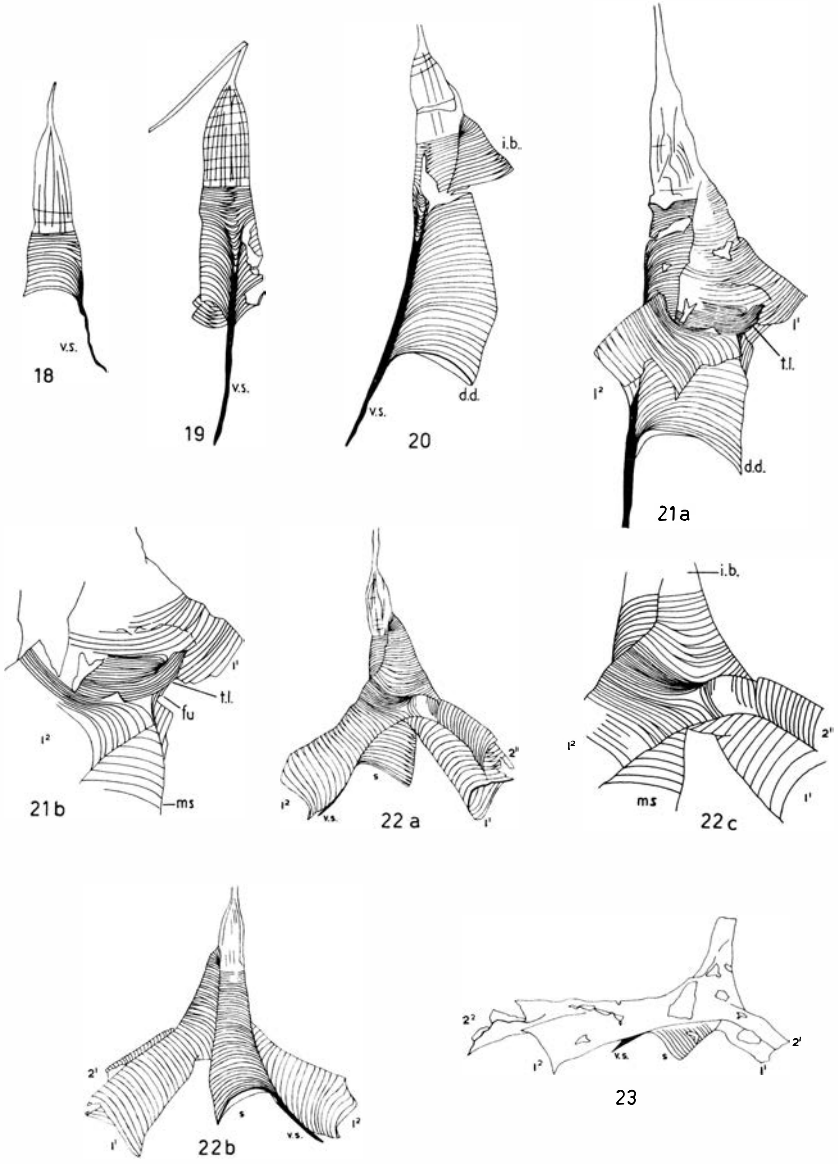
Two distal stipe fragments recovered do not agree precisely with Bulman's description. Öl. 1188 (Fig. 17*a*) slightly exceeds the quoted dorso-ventral width (0.7 mm, as against 0.6 mm) and possibly has fewer thecae per cm—three are present in 2.9 mm, suggesting 10–11 per cm as compared with a stated range of 12–14. However, the thecae—expanding aperturally, lacking a ventral process, and overlapping 0.33 to 0.5 their length—agree in form with those of *D. formosus*. In this specimen (Fig. 17*b*), the growth lines on the lower (dorso-) lateral walls of the thecae assume a fan-like form, which is connected with the distal extension of the dorso-lateral edges of the apertural margins.

A second distal fragment differs from BULMAN's description only in dorso-ventral stipe width, which is 0.75 mm.

The prosicula (Figs. 18, 19) is normally parallel-sided, attaining a length of 0.30 mm and a diameter, at the distal margin, of 0.12 mm. Öl. 1191 (Fig. 21 *a*) is exceptional in this respect, having a prosicula 0.37 mm long and 0.16 mm wide at the margin. The structure of the prosicula is clearly preserved in only one instace (Fig. 19); here, the spiral thread is right-handedly coiled, and at least 8–10 primary longitudinal rods, and several more secondary rods, are evident. Unlike the diplograptid prosiculae figured by KRAFT (1926) and WALKER (1953), the distance between successive whorls of the spiral does not increase to a maximum and then decrease again to the distal margin, but rather there is a rapid increase to a maximum which is maintained, with but little variation, to the margin. A stout nema is given off from the proximal tip of the prosicula.

The mature sicula attains a length of about 1.2 mm (1.65 mm in Öl. 1192, Fig. 22*a*, *b*) and an apertural width of between 0.30 mm and 0.40 mm. A characteristic curvature towards the virgellar side affects the distal 0.5 mm of the sicula (Figs. 22*a*, *b*, 23). A prominent virgella spine projects for a distance of up to 0.5 mm beyond the level of the sicula aperture; a slight lip is developed on the anti-virgellar side of this aperture, but otherwise it remains unornamented. The virgella originates within 0.10 mm of the base of the metasicula (Figs. 18, 19, 20), but the downward deflection of the growth bands, as they approach the zig-zag suture on the virgellar side, is evident after the development of the first two or three fuselli. At first, thickening is noted along two zones on either side of the suture, these converge and unite distally to produce the prominent virgella spine. The growth lines on the anti-virgellar side also show an appreciable downward curvature as they approach the suture on that side—this is reflected in the lip on the anti-virgellar side of the apertural margin of the sicula (Figs. 19, 20, 21 *a*).

DEVELOPMENT.—The initial foramen appears in the prosicula, on the anti-virgellar side; the upper rim is situated 0.20–0.25 mm below the base of the nema. The development of the initial bud from the foramen (Fig. 20) coincides approximately with the completion of growth of the sicula. The direction of growth of this bud is downwards, towards the aperture of the sicula. Growth proceeds by the addition of half rings to the growing edge, whilst the bud



Figs. 18–23: *Didymograptus formosus* BULMAN, 1936. (18) Immature sicula. × 45. Hälludden – 118 – 120 D; Öl. 1189*a*, (19) Slightly more advanced growth stage. × 45. Hälludden – 118 – 120 D; Öl. 1189*b*. (20) Mature sicula with initial bud. × 43. Hälludden – 118 – 120 D; Öl. 1190. (21) Growth stage including origin of th 2^1, reverse aspect; (21 *a*) complete specimen, × 43; (21 *b*) part of same enlarged, × 59. Hälludden – 118 – 120 D; Öl. 1191. (22) Early growth stage including foramen of th 2^2; (22 *a*) reverse aspect, × 24; (22 *b*) obverse aspect, × 24; (22 *c*) part of 22 *a* enlarged to show details of growth lines, × 47. Hälludden – 113 – 116 D; Öl. 1192. (23) Damaged proximal end. × 18. Hälludden – 118 – 120 D; Öl. 1193. *d.d.:* dorsal denticle; *fu:* initial fuselli of th 2^1 (Fig. 21 *b*); *i.b.:* initial bud; *ms:* metasicula; *s:* sicula; *t.l.:* transverse ledge; *v.s.:* virgella spine.

undergoes a progressive increase in width so that the right- and left-hand edges (facing the anti-virgellar side of the sicula) extend onto the obverse and reverse walls of the sicula, respectively.

About 0.25 mm below the upper rim of the initial foramen, a sudden increase in the transverse dimension of the bud, achieved largely by the encroachment of the reverse edge onto the reverse wall of the sicula, marks the first stage in the appearance of th1^{2} (Fig. 21*a*, *b*).

Th^{1} continues the downward direction of growth of the initial bud, by the addition of half rings and wedge-shaped growth bands to within 0.30 mm of the aperture of the sicula, where it assumes the form of a complete tube and diverges from the sicula to grow obliquely out and down (Figs. 22*a*, *b*, 23). This divergence is accentuated by the distal curvature of the sicula towards the virgellar side; the included angle varies from 90° in Öl. 1193 (Fig. 23) to 40° in Öl. 1192 (Fig. 22*a*, *b*). The subsequent growth of th1^{2} is obliquely across the lower half of the sicula, and at such an angle as to pass out along the virgella spine, the tip of which characteristically projects from the middle of the free ventral wall of th1^{2} (Figs. 22*a*, *b*, 23).

The angle enclosed by the two initial thecae, where they leave the sicula, is 130° in Öl. 1193 (Fig. 23), and 90° in Öl. 1192 (Fig. 22*a*, *b*); in all instances, the angle is appreciably less than that quoted by BULMAN (150°). Thus, the initial angle of divergence of the stipes in *D. formosus* may lie within an observed range of 90° to 150°.

Th2^{1} is derived from th1^{2} almost immediately following the appearance of the latter (Figs. 21*a*, *b*, 22*a*, *c*). In its proximal part, whilst still attached to the sicula, th1^{2} is a half-tube or hood-like structure, similar to the initial bud and the proximal part of th1^{1}. Shortly after its separation, and as a prelude to the development of th2^{1}, the right-hand growing edge of th1^{2} (viewing the sicula from the anti-virgellar side) is transversely extended as an arched ledge (*tl*, Fig. 21*b*); thereafter, however, growth of the edge proceeds towards the virgellar margin of the sicula aperture, subparallel to the left-hand edge of th1^{2}. As a result, a 'gulf' is produced in the right-hand wall of the theca, and it is here that the first fuselli of th2^{1} are laid down—vertically (*fu*, Fig. 21*b*). Their upper edges lie abruptly against the margin of the transverse ledge, whilst the lower edges are fused to the reverse lateral wall of th1^{1}, at or about the level at which the latter diverges from the sicula. In detail, the growth of th2^{1} is at first slightly upwards (Figs. 22*a*, *c*), but the direction quickly changes, and growth follows the dorsal wall of th1^{1}.

After the appearance of th2^{1}, the growth of the two stipes is continued independently. In *D. formosus*, two crossing canals are developed and th1^{2} is dicalycal: th2^{1} originates shortly after the separation of th1^{2} from th1^{1}; th2^{2} is produced within 0.25 mm of the aperture of th1^{2}. This species thus exhibits the *extensus* stage of the isograptid type of proximal end development.

REMARKS.—The similarity which exists between the proximal end growth

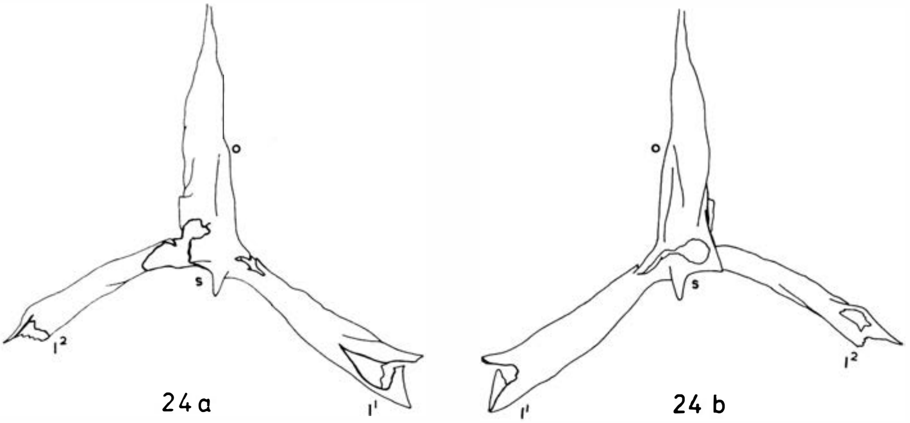


Fig. 24: *Didymograptus* nov. sp. *a* aff. *gracilis* TÖRNQUIST, 1890. (24) Proximal end. (24*a*) reverse aspect; (24*b*) obverse aspect. ×36. Hälludden −110 − 113 D; Öl. 1194. *o:* origin of initial bud; *s:* sicula.

stage figured by HOLM (1895, pl. 11, figs. 4–6) and an early growth stage of *D. formosus* is so striking that the lack of any trace of th2^1 in the former can, perhaps, best be regarded as being due to the retarded development of that theca.

KOZŁOWSKI (1953, footnote on p. 208) has stated that the virgella spine in *D. formosus* is, in fact, a denticle comparable, in all respects, with the process developed on the ventral apertural margin of the sicula in the dendroids and the more primitive graptoloids. It is clearly apparent in Figs. 18–20 that the structure present in *D. formosus* is a true graptoloid virgella (of the type seen to advantage in the Diplograptidae, for example), which is extended beyond the sicula aperture as a prominent spine.

Didymograptus* n. sp. *a* aff. *D. gracilis TÖRNQUIST, 1890

Fig. 24

1895 *Didymograptus gracilis* TÖRNQUIST, mut.—HOLM p. 334, pl. 11, figs. 7, 8.
1895 *Didymograptus gracilis* TÖRNQUIST, mut.—HOLM, p. 441, pl. XIII, figs. 7, 8.
1901 *Didymograptus gracilis* (TÖRNQUIST, mut.)—TÖRNQUIST, p. 22.
1936 *Didymograptus gracilis* TÖRNQUIST, mut.—BULMAN, pp. 26, 27, pl. 1, figs. 8–12; text fig. 7.
1960 *Didymograptus* aff. *gracilis* TÖRNQUIST—JAANUSSON, p. 341, Table 8.

FIGURED MATERIAL.—No. Öl. 1194.

LOCALITY AND HORIZON.—Hälludden: −110 − 113 D.

DESCRIPTION.—A single, damaged proximal end of this species has been recovered (Figs. 24*a*, *b*).

The sicula is short and slender, 0.78 mm long and 0.16 mm wide at the aperture. A short ventral denticle is developed on the apertural margin, 0.1 mm in length. The distal margin of the prosicula cannot be identified.

The initial bud originates 0.3 mm below the base of the nema, on the ventral side of the sicula; it grows down to the level of the aperture, where it gives rise to th1^1 and th1^2. Th1^1 diverges abruptly from the sicula at an angle of c. 55°. A slight denticle is developed on the ventral edge of this theca; the dorso-ventral width of the stipe is 0.2 mm at this level. Th1^2 is directed horizontally across the sicula, so that th1^1 and th1^2 at first enclose an angle of 145°; beyond the sicula, the dorsal wall of th1^2 is convexly curved, however, giving an initially declined rhabdosome, whilst that of th1^1 shows slight concave curvature—resulting in an asymmetrical proximal end. The origin of th2^1 is not clearly indicated, but appears to be close to the aperture of th1^1, where a slight swelling is evident on the dorsal wall of the stipe. A similarly-positioned swelling on th1^2 probably marks the point of origin of th2^2. The primitive *bifidus* stage of the dichograptid type of development is portrayed by this specimen.

Discussion.—This single specimen agrees with Holm's "mutation" in having the stipes leaving the sicula at the same level and in possessing an initially declined direction of growth.

Topotypes of *D. gracilis*, etched out of the Lower *Didymograptus* Shale by Dr. R. Skoglund, are not conspecific with the Öland material. Dr. Skoglund (*in litt.* 1963) stresses two important morphological differences, which are that in *D. gracilis* the stipes leave the sicula at different levels and that the prothecal part of th2^1 is extremely long.

***Didymograptus* cf. n. sp. *a* aff. *D. gracilis* Törnquist, 1890**

Figs. 25, 26

1936 *Didymograptus* cf. *D. gracilis* Törnquist, mut.—Bulman p. 27, pl. 1, fig. 12.

Figured Material.—Spec. No: Öl. 1195*a*, *c*.

Locality and Horizon.—Hagudden: 0 + 15D, + 10 + 15D.

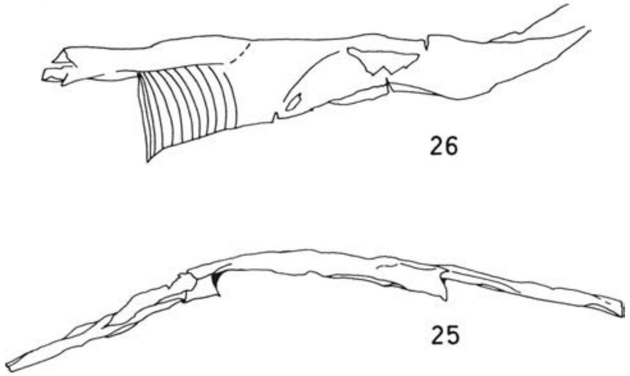
Description.—Fragments of stipe, of extremely slender dimensions, are identified with a specimen from the Holm Collection (No. 1265) which has been compared by Bulman (1936) with *D. gracilis* Törnquist, mut. Holm.

Dorso-ventral stipe width, at thecal apertures, ranges from 0.20–0.24 mm, and 0.75 of this is accounted for by the height of the aperture. Thecal length varies from 1.07–1.33 mm and the thecae are eight times as long as wide at the aperture. Overlap is of the order of 0.14–0.17. The apertural margin is straight to slightly concave, with a minute, though distinct, ventral denticle. The number of thecae developed per cm, as deduced from the fragments, none of which includes more than two thecal apertures, is 9–12.

***Didymograptus* n. sp. *b* aff. *D. minutus* Törnquist, 1879**

Figs. 27–29

1895 *Didymograptus minutus* Törnquist, mut.—Holm, p. 332, pl. 11, figs. 1–3.
1895 *Didymograptus minutus* Törnquist, mut.—Holm, p. 440, pl. 13, figs. 1–3.
1929 *Didymograptus minutus* Törnquist, mut.—Stubblefield, p. 285.



Figs. 25–26: *Didymograptus* cf. nov. sp. *a* aff. *gracilis* TÖRNQUIST, 1890. (25) Stipe fragment. ×36. Hagudden +10+15D; Öl. 1195*c*. (26) Thecal aperture and origin of next following theca. ×65. Hagudden +10+15D; Öl. 1195*a*.

1933 *Didymograptus minutus* TÖRNQUIST, mut.—BULMAN, p. 6, pl. 1, fig. *b*.
1936 *Didymograptus minutus* TÖRNQUIST, mut.—BULMAN, pp. 28, 29, pl. 1, figs. 1–4.
1954 *Didymograptus minutus* TÖRNQUIST, mut.—KOZŁOWSKI, pp. 426–7, fig. 1*C*.
1955 *Didymograptus minutus* TÖRNQUIST, mut.—BULMAN, p. V57, fig. 38.
1960 *Didymograptus* cf. *minutus* TÖRNQUIST—JAANUSSON, p. 341, Table 8.

FIGURED MATERIAL.—Spec. Nos: Öl. 1196–Öl. 1198.

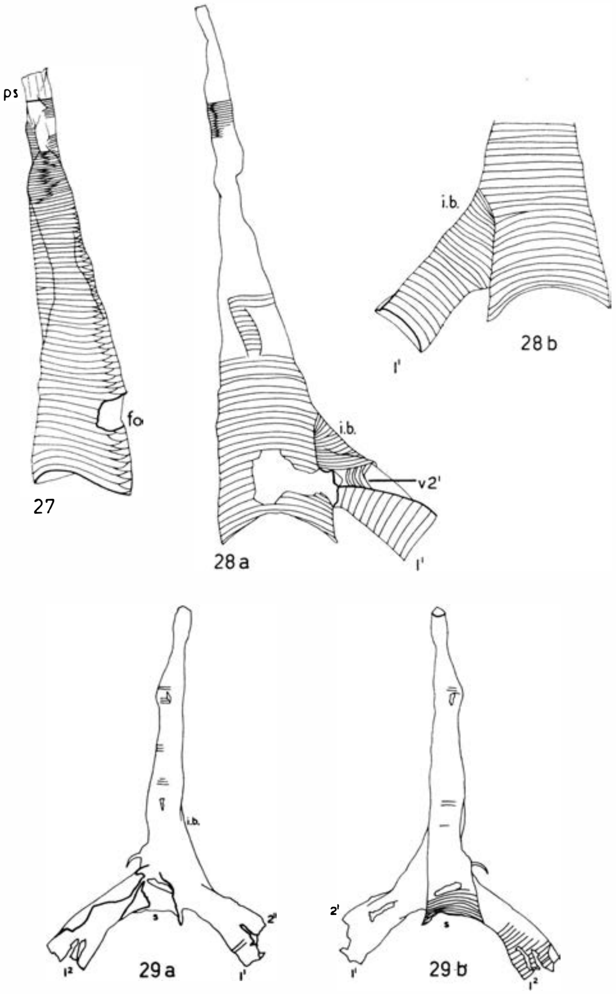
LOCALITY AND HORIZON.—Hälludden: +18+22D, +23+26D; Hagudden: 0−8D, 0+15D.

DESCRIPTION AND DEVELOPMENT.—The material recovered comprises early growth stages and a damaged proximal end.

In all cases, the base of the nema is missing, so that the true length of the sicula is not known; the maximum preserved length is 1.85 mm. The greatest length of prosicula preserved (Fig. 28*a*) is 0.33 mm; the detailed structure is not evident, except for the presence of longitudinal rods in Öl. 1196 (Fig. 27).

The metasicula expands gradually to the aperture (Figs. 28*a*, 29*b*), which averages 0.3 mm in width. The growth lines on the metasicula are at first quite disorderly, and it is not until some distance below the prosicular margin (0.3 mm below in Öl. 1196, Fig. 27) that a dorsal and ventral zig-zag suture can be identified. The sicula aperture is concave and is provided with two slight denticles, one dorsal and one ventral, with the latter longer than the former.

The sicula may show a slight degree of curvature and irregularities in width may occur, though these latter can usually be attributed to contraction of the periderm. It is perhaps worthy of note, however, that in HOLM's (1895) specimens, the sicula contracts noticeably above the level of the initial bud, and remains narrow to the base of the nema, into which it merges almost imperceptibly; in the present material, on the other hand, a gradual increase in width is maintained throughout the length of the metasicula, from its origin to the aperture.



Figs. 27–29: *Didymograptus* nov. sp. *b* aff. *minutus* TÖRNQUIST, 1879. (27) Sicula with initial foramen. ×43. Hälludden + 18 + 22 D; Öl. 1196. (28) Proximal end growth stage including th 2^1; (28*a*) reverse aspect; (28*b*) obverse aspect. ×43. Hälludden + 23 + 26 D; Öl. 1197. (29) Proximal end; (29*a*) reverse aspect; (29*b*) obverse aspect. ×24. Hagudden 0 − 8 D; Öl. 1198. *fo:* initial foramen; *i.b.:* initial bud; *ps:* prosicula; *s:* sicula; $v2^1$: vertically-set fuselli of th 2^1.

The growth of the sicula is not completed by the time the initial foramen is produced (Fig. 27), but it must be greatly advanced by this stage, for the upper rim of the foramen in the mature sicula is within 0.5 mm of the sicula aperture. The diameter of the foramen (Fig. 27) is 0.12 mm; it is situated approximately 1.0 mm below the distal margin of the prosicula, well within the lower half of the sicula. The initial bud is very short (Fig. 28*a*) and it rapidly expands in width to accommodate the origin of the first three thecae of the rhabdosome.

Th1^1 leaves the sicula at the level of the aperture, at an angle of approximately 90°, but this angle is drastically reduced by curvature of the theca as its aperture is approached (Figs. 29*a*, *b*). In Fig. 28*a*, it is noted that the dorsal wall of th1[1] is infolded for the reception of the proximal part of th2[1]. The very first fuselli of this latter are vertically-set half rings; at a later stage, a dorsal suture is produced, th2[1] then having the form of a split tube, and it remains as such until it becomes free of contact with the first theca. Th1[2], originating at the same level as th2[1], grows obliquely across the sicula and leaves it at the level of the aperture (Figs. 29*a*, *b*) and at an angle of about 45°, obscuring the dorsal denticle in the process. As in the case of th1[1], subsequent curvature reduces the angle of inclination to the sicula, though the amount of recurving achieved by the first theca of each stipe is not so great as in the material described by HOLM (1895). In Öl. 1198 (Figs. 29*a*, *b*), th1[2] is incomplete aperturally, but the origin of th2[2] is preserved at a distance of 0.53 mm from the sicula, measured along the dorsal wall of the theca.

DISCUSSION.—The present Öland material approaches most closely that described by HOLM (1895) as *Didymograptus minutus* mut., though slight differences exist in sicular shape and in the degree of divergence of the initial thecae. Dr. SKOGLUND informs me (*in litt.* 1963) that the Öland specimens are not conspecific with topotypes of *D. minutus*, which latter have a *bifidus* stage of proximal end development.

Genus *Aulograptus* gen. nov.

TYPE SPECIES.—*Didymograptus cucullus* BULMAN, 1932.

DIAGNOSIS.—Rhabdosome didymograptid; stipes pendent. Thecae of climacograptid type, with free ventral wall parallel to dorsal stipe margin throughout the rhabdosome; aperture distally directed or slightly extrovert; margin may be provided with a distinct rim and a genicular list may be developed. Development: *extensus* stage of isograptid type in some.

SPECIES.—*Didymograptus cucullus* BULMAN, 1932.
Didymograptus obscurus EKSTRÖM, 1937.
Didymograptus climacograptoides BULMAN, 1931.
Holmograptus ? orientalis MU, 1957.
?*Didymograptus*? sp. *C* JAANUSSON, 1960.

REMARKS.—While the thecal excavations in *D. obscurus*, seen in profile, are as shallow as in *D. cucullus*, there is no trace of a genicular list or of a subapertural spine in EKSTRÖM's material, though the possibility of this being a preservational feature cannot be overlooked.

The fragments of stipe described by JAANUSSON (1960) as *Didymograptus*? sp. *C* appear to differ from *D. obscurus* only in having fewer thecae per cm. The thecal aperture is semi-ovoid (cf. JAANUSSON, 1960, p. 340, in respect of *D. obscurus*) and extrovert and the margin is developed as a raised rim without lists or spines. JAANUSSON (1960) notes that "the identity of *D. cucullus* and *D.*

obscurus seems possible" (p. 341), though he makes no mention of the similarity in thecal form existing between *D. obscurus* and *Didymograptus*? sp. *C.*

Holmograptus ? *orientalis* appears to belong in *Aulograptus*, though thecal details in MU's species are obscure.

The preservation of the type material of *Didymograptus climacograptoides* is such that the form assumed by the thecae is not clear, though it seems likely that they are of climacograptid type with distinct geniculum and distally directed aperture.

DERIVATIO NOMINIS.—From the Gr. *aulos* (αὐλός): a wind instrument in the form of a hollow cylinder with holes along its length, having reference to the flute-like form of the stipes in the type species.

Aulograptus cucullus (BULMAN, 1932)

Figs. 30–33

1932 *Didymograptus cucullus* n.sp.—BULMAN, pl. 1, figs. 1–8, text fig. 1.
1936 *Didymograptus cucullus* BULMAN—BULMAN, p. 23.
1950 *Didymograptus cucullus* BULMAN—BULMAN, p. 4.
1954 *Holmograptus cucullus* BULMAN—KOZŁOWSKI, pp. 424, 434.
1960 *Didymograptus cucullus* BULMAN—JAANUSSON, pp. 340–341, Table 8.

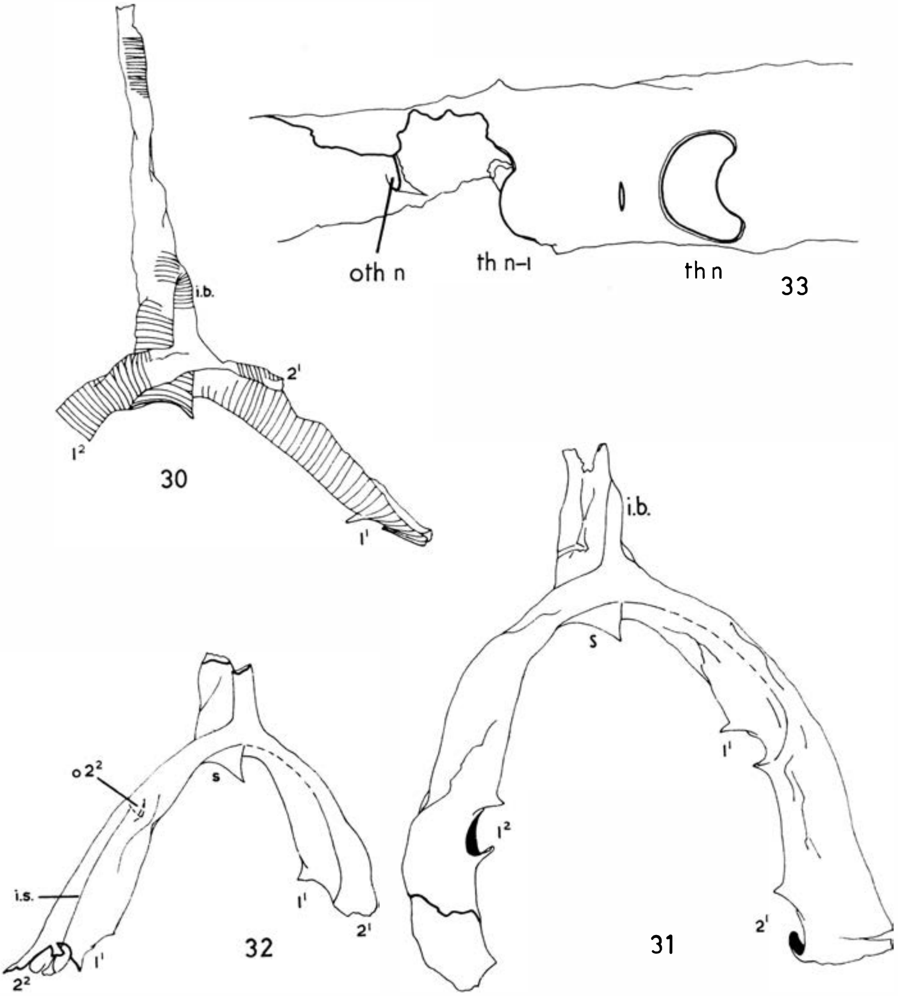
FIGURED MATERIAL.—Spec. Nos: Öl. 1202–Öl. 1205.

LOCALITY AND HORIZON.—Hälludden: −135 −140D, −118 −120D, −100D.

DIAGNOSIS.—(amended): Small, pendent rhabdosome, with slender stipes up to 7.3 mm in length; dorso-ventral stipe width increasing distally to 0.66 mm. Thecal aperture extrovert; margin with distinct rim continuous with genicular list; sub-apertural spine developed; 13–14 thecae per cm; overlapping 0.33 distally. Sicula narrow and conspicuous, 1.6 mm in length, 0.22–0.33 mm in width at aperture; provided with ventral and slight dorsal denticles. Initial bud appears well within lower half of sicula; th1^2 dicalycal; *extensus* stage of development.

DESCRIPTION.—The complete sicula is unknown; characteristically, it is the prosicula which is missing, while the apertural portion is usually preserved intact. The preserved length in Öl. 1202 (Fig. 30) is 1.5 mm, and the apertural width is 0.22 mm—indicating a long, parallel-sided sicula. The preserved length of the other siculae recovered is much less, though the apertural width may be as great as 0.33 mm (Fig. 31); squashing may account for some of the variation noted in this dimension. The margin of the sicula aperture is strongly concave and is provided with both a ventral and a dorsal denticle—the former larger than the latter. The prosicula is entirely unknown; the metasicula is probably almost completely preserved in Öl. 1202 (Fig. 30), for the growth lines close to the proximal extremity are very irregular, and it is some distance before regular dorsal and ventral zig-zag sutures are established.

The stipes are narrow at their origin, and the dorso-ventral width of stipe '1' where it leaves the sicula (0.25 mm in Fig. 31) is appreciably greater than



Figs. 30–33: *Aulograptus cucullus* (BULMAN, 1932). (30) Damaged proximal end growth stage. × 36. Hälludden – 118 – 120D; Öl. 1202. (31) Proximal end of rhabdosome. × 25. Hälludden – 118 – 120D; Öl. 1203. (32) Proximal end showing degree of thecal overlap. × 26. Hälludden – 118 – 120D; Öl. 1204. (33) Stipe fragment showing degree of thecal overlap distally. × 35. Hälludden – 118 – 120D; Öl. 1205. *i.b.*: initial bud; *i.s.*: interthecal septum; *o*2^2: origin th 2^2; *o th'n'* :origin th'n'; *s*: sicula.

that of stipe '2' (0.16 mm in Fig. 31) in a corresponding position. The stipes enlarge distally, so that at the level of the aperture of th2^1 (Fig. 31), the width is 0.45 mm. The greatest dorso-ventral width recorded is 0.66 mm. Öl. 1205 is a stipe fragment 7.3 mm in length and showing distinct curvature consistent with the attainment of a pendent rhabdosome. In this fragment, 7 thecae are preserved in a stipe length of 5.4 mm, suggesting 13 thecae per cm.

In ventral view, the thecal apertures are transversely elongate while in profile they are seen to be slightly extrovert and only shallowly concave so that the degree of excavation is negligible. The apertural margin is bordered by a distinct rim which is continuous with a pronounced genicular list; a sub-apertural (proximal) spine or flange is typically developed (see Fig. 31).

Interthecal septa are seldom preserved, and evidence of their former presence, by a feature such as a groove on the lateral walls of the stipe, is usually lacking. A septum (*i.s.*) can be seen, however, in Fig. 32, in which in addition, the internal orifice ($o2^2$), linking th1^2 and th2^2, is clearly visible through the transparent periderm. In Öl. 1205 (Fig. 33), no trace of the interthecal septa remains, except for the rim of the orifice (*oth‘n’*) at the origin of th‘n’—the presence of this enables the thecal length and the amount of overlap to be measured: 1.2 mm and 0.33, respectively.

Development.—The initial bud is produced from the ventral side of the sicula (Figs. 30–32); the upper rim of the initial foramen is situated 0.7 mm above the level of the sicula aperture in Öl. 1202 (Fig. 30); the foramen is thus well within the lower half of the sicula. The initial bud grows down the ventral wall of the sicula, to a level just above that of the aperture, where it gives rise to th1^1 and th1^2. Th1^1 continues the downward direction of growth of the bud for a very short distance, to the sicula aperture, at which level it diverges from the sicula. Th1^2 grows obliquely across the sicula, and leaves it at the level of the aperture on the dorsal side—effectively obscuring the dorsal denticle in the process. Th2^1 arises from th1^2 almost immediately upon the origin of this latter from th1^1. Th1^2 is, therefore, dicalycal, and the *extensus* stage of the isograptid type of proximal end development is portrayed. Th1^1 and th1^2, though diverging initially, converge as their apertures are approached (Fig. 31) and the stipes quickly adopt the pendent attitude characteristic of the species.

Discussion.—Bulman (1950*b*) suggested that "*D. cucullus* may eventually be shown to be conspecific with *D. climacograptoides*" (p. 4), and that this latter was almost certainly conspecific with *D. obscurus* Ekström.

A re-investigation of available material by Jaanusson (1960) was inconclusive, owing to the lack of suitably preserved specimens of the two latter species; thus, he writes that "the identity of *D. cucullus* and *D. obscurus* seems possible, but cannot be conclusively proved until details of the apertural margin are known in the latter species" (p. 341). The writer has also examined this material and is disposed to agree with Dr. Jaanusson that a direct comparison of *A. cucullus* and *A. obscurus* is impracticable in view of the very different modes of preservation involved. However, the writer would refer to *A. cucullus* material from the Zone of *D. bifidus* in Britain which has been identified as *Didymograptus climacograptoides* Bulman (see Shotton, 1935). Though flattened, apertural details are well preserved in this material and in several instances genicular lists and proximal (ventral) flanges are present, but when these have not been preserved the specimens agree in all respects with *A. obscurus*. On this evidence, it is believed that *A. obscurus* is a junior synonym of *A. cucullus*.

With regard to *D. climacograptoides*, Jaanusson (1960, p. 341) has noted that "the available material is too poorly preserved to permit the observation of details of the shape of the thecal aperture, and a slightly too high number of thecae in a given unit of length may indicate specific differences". To this, the writer would add that the greater depth of the apertural excavations in *D. climacograptoides* compared with *A. cucullus* is, in itself, an important basis of distinction and would seem to indicate a distally directed aperture in the former species.

Mu (1957) described *Holmograptus* ? *orientalis* from the Ningkuo Shale of China and noted that "in the essential characters this species closely resembles *H. cucullus* (Bulman) from Sweden" (p. 427), differing chiefly in possessing more thecae per cm (16, as against 13–14 in *A. cucullus*). If, however, the thecal number in *H.* ? *orientalis* is calculated from the text and plate figures (1957: text fig. 13 and pl. 4, figs. 9–12), which are stated to be at a magnification of × 5, a value comparable with that in *A. cucullus* is obtained, and the identity of these two species seems likely.

Dichograptids of Unknown Generic Affinity

Dichograptid sp. *a* gen. et sp. indet.

Figs. 34–39

Figured Material.—Spec. Nos. Öl. 1215–Öl. 1219.

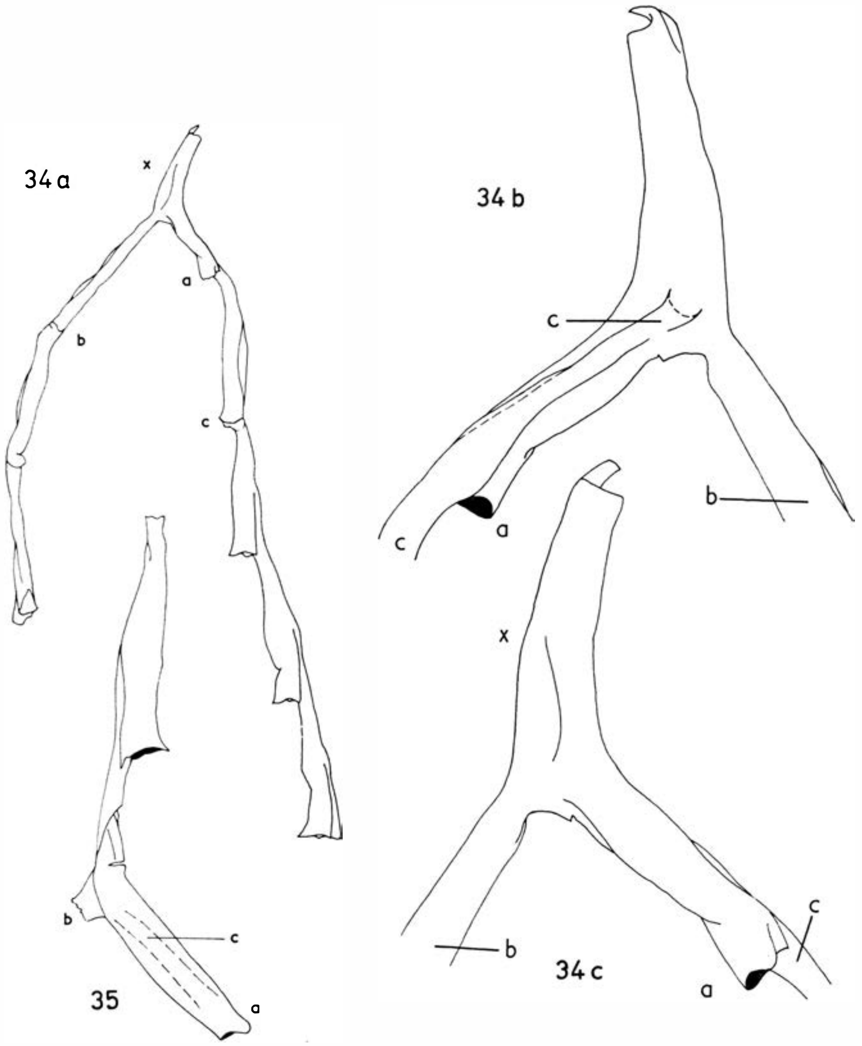
Locality and Horizon.—Hälludden: −118 −120D.

Description.—The form of the complete rhabdosome is unknown. The largest fragment recovered is the proximal end specimen Öl. 1217 (Fig. 36), which comprises a sicula and two, short, first order stipes, one of which bifurcates to give two, longer (but incomplete), second order stipes; the stipes are all contained more or less in a horizontal plane.

The sicula is relatively short (0.74 mm) and gradually expanding in form, from the base of the nema to the aperture, where it is 0.2 mm in diameter. The distal margin of the prosicula cannot be determined. The sicula aperture is provided with a distinct ventral denticle, broad and roundly-terminated.

The length of the first order stipes is 1.5 mm; at this distance from the sicula, dichotomy occurs, and the resulting stipes diverge at an angle of 90°. The preserved length of the longer of the two second order stipes is 4 mm; in this stipe, the dorso-ventral width at the level of the thecal apertures increases from 0.27–0.33 mm distally along the stipe; the thecae number 4 in 3.4 mm, suggesting 11–12 thecae per cm, and overlap 0.25–0.33 their length, which is 1.2 mm.

Stipe fragments recovered which may have occupied a more distal position in the rhabdosome are slightly more robust. In Öl. 1215 (Fig. 34*a*), dorso-ventral stipe width at thecal apertures is 0.33 mm, two-thirds of which is accounted for by the height of the aperture itself. The greatest dorso-ventral



Figs. 34–35: Dichograptid sp. *a* gen. et sp. indet. (34) Branched fragment of rhabdosome; (34*a*) complete specimen, × 18; (34*b*) detail of branching in dorsal aspect. × 67; (34*c*) detail of branching in ventral aspect. × 67. Hälludden – 118 – 120D; Öl. 1215. (35) Branched fragment of rhabdosome. × 35. Hälludden – 118 – 120D; Öl. 1216. *a*, *b*, *c*: theca 'a', theca 'b', theca 'c'; *x*: origin of theca 'b'.

stipe width recorded, at a thecal aperture, is 0.45 mm. The distal thecae are low-lying, the ventral angle not exceeding 10°. Thecal length averages 1.6 mm; the thecae are 7 times as long as the height of the aperture; they overlap 0.25–0.33 their length. In Öl. 1215 (Fig. 34*a*), 9 thecae are developed per cm. The apertural margin is set at 90° to the dorsal wall and is slightly concave (Fig. 39); in detail, it may show a pair of small, lateral lappets (Fig. 38). The dorsal stipe margin is generally straight, except for slight swellings developed at the thecal origins (Fig. 38). The two stipes in Öl. 1215 (Fig. 34*a*) are laterally curved

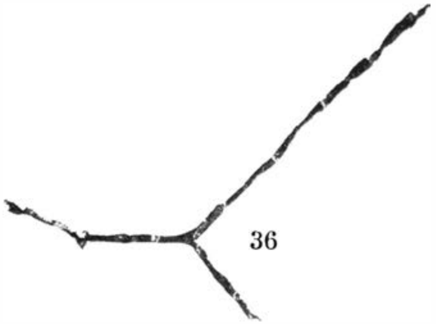


Fig. 36: Dichograptid sp. *a* gen. et sp. indet. (36) Proximal end of rhabdosome in ventral aspect. × 10. Hälludden − 118 − 120D; Öl. 1217.

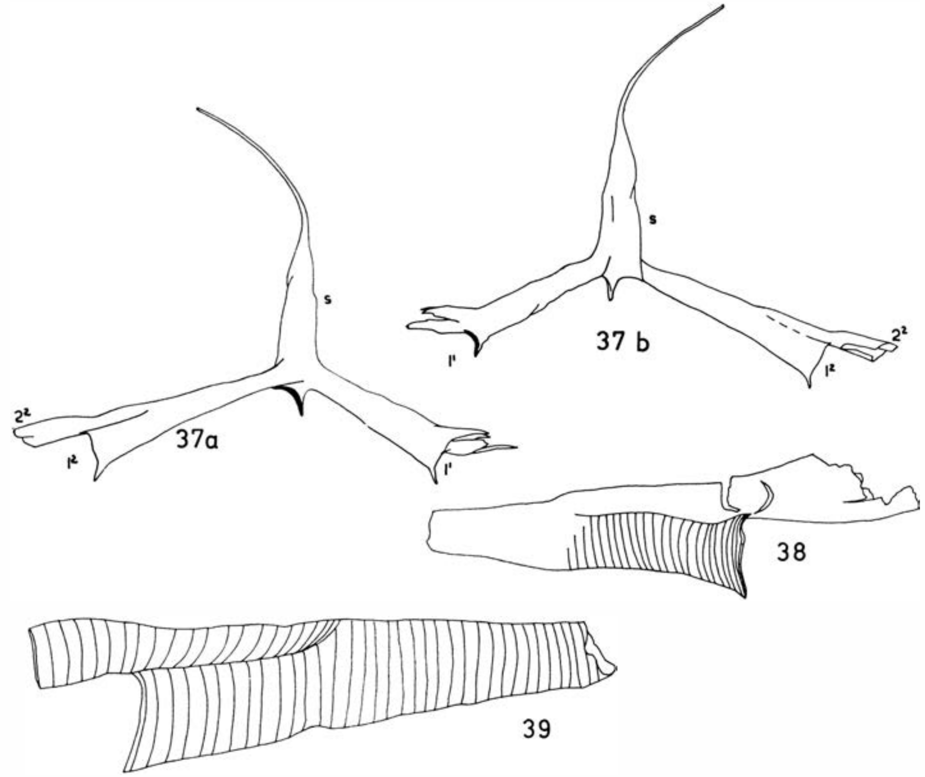
beyond their origin, and quickly become subparallel; no dorsal or ventral stipe curvature is present in any specimen.

In the distal fragment Öl. 1215 (Fig. 34), a single instance of rhabdosomal branching is preserved. It is not certain how this division has been achieved, though it may have been effected in the same manner as the primary division in the dichograptid type of proximal end development. The two branches probably originate at the point 'x' (Figs. 34*a*, *c*), where th'b' appears to bud off from th'a', but actual separation of the branches is delayed until the level of origin of th'c' (Fig. 34*b*). Th'c' seems to bud off from th'b', after which the two stipes develop independently and th'b' is consequently dicalycal. At the separation of the branches, th'a' is deflected through 45° and the two branches initially enclose an angle of 75° to 80°, but lateral curvature causes them to become parallel by the level of the third thecal aperture on each branch.

DEVELOPMENT.—The initial bud originates well within the upper half of the sicula, 0.25 mm below the base of the nema, and on the ventral, or denticled, side. Growth of the bud is directed down the ventral wall, towards the sicula aperture. The point of origin of th1^2 (and hence of th1^1) is obscured by wrinkling of the periderm though it is undoubtedly above, and possibly appreciably above, the level of the sicula aperture. Th1^1 diverges from the sicula, at about the level of the aperture, at an angle of 65°–70°; the aperture of this theca is situated 0.74 mm from the sicula. Th1^2 leaves the sicula at the dorsal margin of the aperture, and the two initial thecae enclose an angle of 140°.

The exact origin of th1^2 has an important bearing on th2^1. The greater thickness of stipe '1', compared with stipe '2', where it leaves the sicula (Fig. 37), is taken to indicate the presence of the proximal part of th2^1 lying against the dorsal wall of th1^1. Depending upon the point of origin of th1^2, th2^1 may be produced from th1^1 (*minutus* stage), if th1^2 arises at the level at which th1^1 diverges from the sicula, or from th1^2 (*extensus* stage), if th1^2 is produced at a higher level, closer to the initial foramen.

DISCUSSION.—No multi-branched dichograptids have been described from



Figs. 37–39: Dichograptid sp. *a* gen. et sp. indet. (37) Proximal end; (37*a*) reverse aspect, ×25; (37*b*) obverse aspect, ×25. Hälludden −118−120D; Öl. 1217. (38) Stipe fragment showing form of thecal aperture. ×35. Hälludden −118−120D; Öl. 1218. (39) Stipe fragment with detail of fuselli. ×66. Hälludden −118−120D; Öl. 1219. *s:* sicula.

the Ontikan limestones, but the underlying Lower *Didymograptus* Shale in Scania has produced a wealth of such forms. Any comparison with these latter, however, must await the recovery of a complete rhabdosome of the Öland species.

REMARKS.—Spec. Öl. 1217 is preserved in two parts; the original specimen (Fig. 36) was broken in order that the sicula and early thecae (Figs. 37*a*, *b*) could be more closely studied.

Dichograptid sp. *b* gen. et sp. indet.

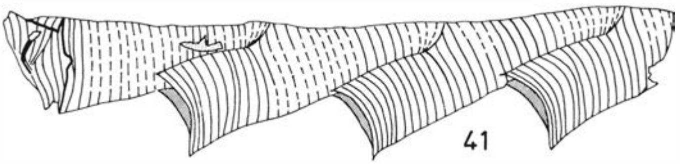
Figs. 40–43

FIGURED MATERIAL.—Nos. Öl. 1220, Öl. 1221 *a*, *b*, *c*.

LOCALITY AND HORIZON.—Hälludden: −135−140D, −118−120D.

DESCRIPTION.—The material recovered comprises only fragments of stipe of varying lengths.

The stipes are straight or but slightly curved; thus, in Öl. 1220 (Fig. 40), the



41

40

Figs. 40–41: Dichograptid sp. *b* gen. et sp. indet. (40) Stipe fragment from ? proximal end of rhabdosome. × 18. Hälludden – 135 – 140D; Öl. 1220. (41) Stipe fragment. × 25. Hälludden – 118 – 120D; Öl. 1221*c*.

dorsal stipe margin is convexly curved proximally, but straight distally; furthermore, there is a distal increase in dorso-ventral stipe width in this specimen, suggestive of a near-proximal position in the rhabdosome, which, it is concluded, was most probably declined. Öl. 1221*a* (Fig. 43) and Öl. 1221*b* (Fig. 42), on the other hand, suggest a horizontal or initially deflexed rhabdosome, respectively, for whilst the former has a straight dorsal wall that of the latter is concavely curved. The absence of any evidence of bifurcation of the stipes suggests a two stiped (didymograptid) rhabdosome.

The dorso-ventral stipe width for the material as a whole, and taken at the level of thecal apertures, ranges from 0.66 mm to 1.03 mm; the average width is 0.80–0.85 mm. The thecae are tubular, and each is 3 to 4 times as long as the height of the aperture; the ventral angle ranges from 19°–28°. The free ventral wall is straight or slightly concavely curved, and a short denticle is developed. The apertural margin is concave and inclined proximally, at a high angle. Thecal length averages 1.6 mm distally, where overlap is of the order of 0.5; proximally, the thecae are from 1.30–1.35 mm in length and overlap is reduced to 0.4. The near-proximal stipe fragments suggest the presence of 10 thecae per cm; more distally derived fragments indicate 11 thecae per cm.

DISCUSSION.—The uncertain form of the rhabdosome and the lack of a proxi-

42

43

Figs. 42–43: Dichograptid sp. *b* gen. et sp. indet. (42) Stipe fragment with straight dorsal margin. × 7.5. Hälludden – 118 – 120D; Öl. 1221*b*. (43) Stipe fragment with dorsal margin concavely curved. × 7.5. Hälludden – 118 – 120D; Öl. 1221*a*.

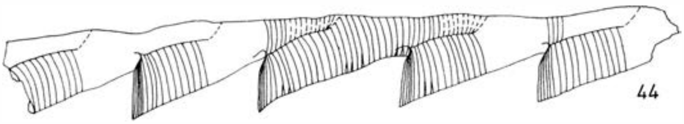


Fig. 44: Dichograptid sp. *c* gen. et sp. indet. (44) Stipe fragment, × 16. Hälludden − 118 − 120D; Öl. 1222.

mal end amongst the material recovered makes a positive identification impossible. However, it is perhaps worthy of note that the probable attitude of the stipes (assuming derivation from a two-stiped rhabdosome), the number of thecae per cm, and the thecal form, all bring to mind *Didymograptus nicholsoni* LAPWORTH.

Dichograptid sp. *c* gen. et sp. indet.

Fig. 44

FIGURED MATERIAL.—No. Öl. 1222.

LOCALITY AND HORIZON.—Hälludden: −118−120D.

DESCRIPTION.—The single specimen recovered is a fragment of stipe of uniform dorso-ventral width, straight throughout its length, and with three thecae preserved complete. The dorsal margin is undulating, but not regularly so, and the specimen presents a distinctly rigid appearance.

Dorso-ventral stipe width is 0.7 mm at thecal apertures and 0.3 mm below the apertures. The thecae are straight, tubular and expand gradually to the aperture; the average thecal length is 1.85 mm; overlap is 0.33; the thecae are 5 times as long as the height of the aperture; and the ventral angle is 20°. The aperture is devoid of a ventral denticle and the plane of the margin is normal to the stipe length, or very slightly inclined distally; the dorso-lateral parts of the margin are distinctly concave, while the remainder is straight or gently convex. Three thecae are developed in 0.3 mm.

DISCUSSION.—Assuming derivation from a two-stiped rhabdosome, this specimen can be compared with *Didymograptus affinis* NICHOLSON in the number of thecae per cm and the angle of inclination of the thecae to the dorsal wall, but differs in having a greater thecal length and more robust stipes.

The form of the apertural margin is similar to that described by HOPKINSON & LAPWORTH (1875) in material which they attribute to *D. affinis* NICHOLSON (but which ELLES & WOOD have referred to *D. nicholsoni* LAPWORTH) except that the plane of the aperture is normal to the elongation of the stipe in the Öland specimen, rather than inclined distally at 120°.

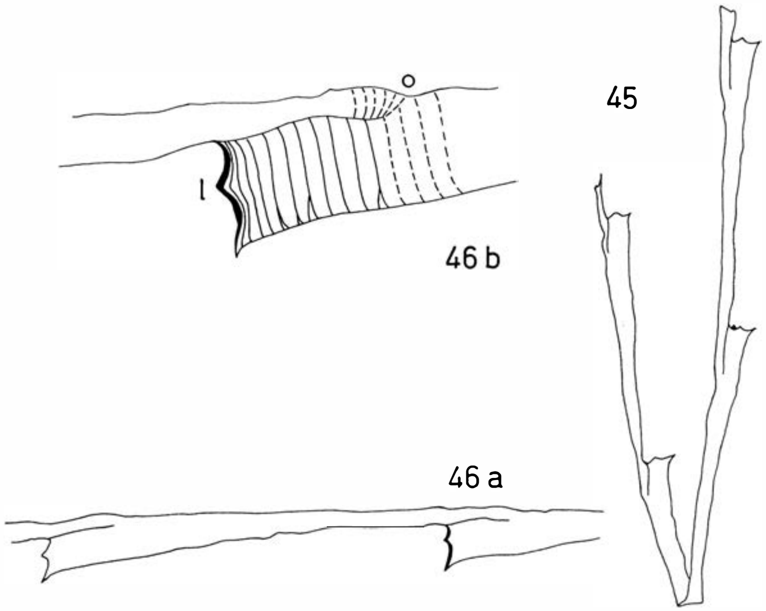
Dichograptid sp. *d* gen. et sp. indet.

Figs. 45, 46

FIGURED MATERIAL.—Nos. Öl. 1213, Öl. 1214.

LOCALITY AND HORIZON.—Hälludden: +18+22D, +23+26D.

DESCRIPTION.—A number of stipe fragments, of exceptionally slender di-



Figs. 45–46: Dichograptid sp. *d* gen. et sp. indet. (45) Regeneration of rhabdosome, × 25. Hälludden + 23 + 26 D; Öl. 1213. (46) Stipe fragment; (46*a*) complete specimen, × 36; (46*b*) part of same enlarged showing details of thecal aperture, × 100. Hälludden + 23 + 26 D; Öl. 1214. *l:* lappet; *o:* thecal origin.

mensions and showing little or no original curvature, have been recovered. The form of the complete rhabdosome and the details of the proximal end are not known.

Thecal length varies from 1.7–1.8 mm, and overlap is of the order of 0.12–0.14; the angle of inclination of the ventral wall is 8°–10°. Dorso-ventral stipe width, at thecal apertures, ranges from 0.18–0.22 mm; the height of the aperture accounts for 0.75 of this dimension. The thecae are from 10 to 12 times as long as they are wide at the aperture. The fragments of stipe are short, so that the number of thecae per cm cannot be stated with certainty, though a figure of 6 to 7 is probably correct. The apertural margin of each theca is diversified by the presence of a pair of laterally-positioned, pointed lappets (Fig. 46*b*); in addition, a minute ventral denticle is developed. The dorsal stipe wall is typically straight.

One fragment (Öl. 1213, Fig. 45) illustrates regeneration of a broken rhabdosome, a process named pseudocladogeny by Urbanek (1963). The specimen is comprised of two stipes, each having two thecal apertures preserved; the stipes are preserved with lateral walls opposed and diverging only slightly from what is assumed to have been the position of fracture of the original rhabdosome. The periderm in the region of divergence is structureless and the actual contact cannot be seen (cf. Urbanek, 1963, text fig. 1 A). The equivalence in form and dimensions of the thecae on the secondary stipe with the single complete theca of the primary stipe suggests that, in this case, it is a distal fragment which has been regenerated. (See URBANEK, 1963, p. 230.)

DISCUSSION.—The several stipe fragments recovered can be compared with a number of slender graptoloids recorded from the Lower Ordovician of Sweden, though they cannot be attributed with confidence to any particular species.

TÖRNQUIST (1911) described specimens of an unknown genus, for which GURLEY had earlier suggested the specific name *chaetoides*. The rhabdosome in this species takes the form of very slender stipes, often occurring in great profusion, but the proximal end is not known. A comparison with the present species shows similarly tenuous stipes and a correspondence in thecal form, except for details of the apertural margin (which may, however, be masked by the mode of preservation). In Genus? *chaetoides*, thecal length is only 1.2 mm, whilst overlap may be as much as 0.5 (BULMAN, 1950*a*: 0.25–0.33).

TÖRNQUIST's (1911) description of *Clonograptus* sp. is too incomplete and too poorly illustrated to permit a detailed comparison with the present material, though it is known to have extremely slender stipes. BULMAN (1950*a*) has described an unnamed species of *Clonograptus* from a proximal end and several stipe fragments, but the description does not include any details of the latter, except to note that they are equally as slender as in TÖRNQUIST's species.

In *Didymograptus gracilis* TÖRNQUIST, 1890, the stipes are, if anything, slightly wider (dorso-ventrally) and the thecae somewhat shorter. There is agreement in the number of thecae developed per cm and also in the form of the thecae, apart from the absence of apertural lappets in *D. gracilis*. The present stipe fragments approach very closely the specimen figured by BULMAN (1936) as pl. 1, fig. 12, but differences include the shorter thecae and the lack of apertural lappets in that specimen. In *Didymograptus filiformis* TULLBERG, 1880, the stipes are extremely slender, but the thecal overlap is greater (up to 0.5) and the thecae are appreciably shorter than in Dichograptid sp. *d*.

The stipe fragments under consideration carry to an extreme the tendency noted in several species to produce a rhabdosome composed of tenuous stipes, and the length of the thecae and their almost negligible overlap, together with the distinctive lappets, provide the easiest means of identification.

REMARKS.—In an extremely lucid thesis on the phenomena of cladial development (cladogeny) and rhabdosomal regeneration (pseudocladogeny) in monograptid graptoloids, URBANEK (1963) has stressed that the latter feature, unlike the former, cannot be accorded any significance in taxonomy. In particular, URBANEK's findings suggest to the writer that the apparently sicula-less Lower. Ordovician genera *Atopograptus* HARRIS and *Janograptus* TULLBERG may have been founded on the regenerated rhabdosomes of normal dichograptids. Thus, it seems reasonable to assume that the "species" *Atopograptus woodwardi* has been established on fragments of *Didymograptus dubitatus* which have suffered regeneration. HARRIS & THOMAS (1935) point out the resemblance in thecal form between *A. woodwardi* and *D. dubitatus*, with the qualification, however, that the stipes in the latter are generally much more slender than are those of the holotype of the former (1935, pp. 294–295). An explanation for this may lie in URBANEK's law of the morphological equivalence of simultaneously budding thecae (1963, p. 230), and the several stipe fragments lacking a "proximal end" which have been attributed to *A. woodwardi* solely on the basis of stipe width should henceforth be interpreted as distal fragments of *D. dubitatus*.

The writer has had an opportunity to examine Swedish material attributed to *Janograptus* and in no instance is there any clear indication of a sicula incorporated in one stipe. On the contrary, the available evidence is strongly suggestive of regeneration. Thus, the type material of *J. laxatus* TULLBERG shows considerable variation in stipe attitude, ranging from deflexed to reflexed (see TULLBERG, 1880*b*, pl. 11, figs. 4 and 5). The specimens attributed to this same species by HADDING (1913) show considerable variation amongst themselves in stipe width and, moreover, there is no distal increase in width along a given stipe, which one would expect to be the case if such a stipe originated in a true proximal end. Again, one of EKSTRÖM's specimens of *J. laxatus* (1937, pl. 6, fig. 8) has stipes which retain a constant width throughout their lengths, but the width of one stipe is 1.25 mm and that of the other 0.75 mm.

The number of specimens of supposed proximal ends of species of *Janograptus* which have been recovered is relatively few. Thus, *J. gracilis* EKSTRÖM is known from two such specimens and *J. dawanensis* LEE from only a single specimen, while it is doubtful whether all material attributed to *J. laxatus* is conspecific. These facts can be adduced as additional support for regeneration.

Perhaps the most convincing evidence that *Janograptus* is not a valid genus, however, is provided by a fragment of rhabdosome isolated by Dr. SKOGLUND from the Lower *Didymograptus* Shale (*P. densus* Zone) at Skattungbyn. There is no trace of a sicula at the origin of the two stipes in this specimen and there can be no doubt that it illustrates regeneration; moreover, the thecal form is identical with that of *D. gracilis* TÖRNQUIST, which latter occurs in extreme abundance at the same horizon. It seems to the writer that there can be little doubt that *Janograptus*, like *Atopograptus*, has been based on regenerated rhabdosomes and is consequently an invalid genus.

Family *Sinograptidae* MU, 1957

Genus *Holmograptus* KOZŁOWSKI, 1954

TYPE SPECIES.—*Didymograptus callotheca* BULMAN, 1932.

DIAGNOSIS.—Rhabdosome didymograptid, stipes declined or deflexed. Proximal thecae of climacograptid type with distinct geniculum. Distally, curvature of thecae reduced or absent; ventral angle 10° to 25°. Prothecal folds (dorsal nodes) typically distinctly developed proximally, and of reduced, equal or increased prominence distally. Apertural ventral spine may be present. Development *extensus* stage in some.

SPECIES.—*Didymograptus callotheca* BULMAN, 1932.
Didymograptus lentus TÖRNQUIST, 1911.
Didymograptus nodosus HARRIS, 1926.
Tylograptus geniculiformis MU, 1957.
Tylograptus geniculiformis var. *flexilis* MU, 1957.
Tylograptus intermedius MU, 1957.
Tylograptus regularis MU, 1957.
Tylograptus globiformis MU, 1957.
Tylograptus spinatus MU, 1957.
Tylograptus spiniformis MU, 1957.
?*Didymograptus spinosus* RUEDEMANN, 1904.
?*Didymograptus spinosus* var. *flexilis* HSÜ, 1934.

D. callotheca BULMAN, 1932, and *T. geniculiformis* MU are in all probability conspecific with *D. lentus* TÖRNQUIST.

According to JAANUSSON (1960), the material from Tossåsen attributed to *D. callotheca* by BULMAN (1950*a*) may belong in *Didymograptus leptograptoides*. In this latter species, the thecae are of leptograptid type, lacking the distinct geniculum and introverted apertural margin characteristic of *Holmograptus* (JAANUSSON, 1964).

JAANUSSON (1964) has noted that, judging from MU's (1957) illustrations, a geniculum does not appear to be developed in *Tylograptus*. If this is the case, *Tylograptus* is not a junior synoym of *Holmograptus* but a final decision on this question must await the opportunity to examine the Chinese material, and, for the present, *Tylograptus* and *Holmograptus* are regarded as congeneric.

THOMAS (1960) compares specimens attributed to *Didymograptus nodosus* with both *Tylograptus intermedius* and *T. regularis* (see 1960, figs. 73 *a*, *b* and 74, respectively), and MU himself notes that ill-preserved specimens of *T. regularis* are very similar to *D. nodosus*. This latter species may also be conspecific with *D. spinosus*. MU (1957) considers his species *T. spinatus* to be closely similar to *D. spinosus*, "but the thecae of the latter species are, as described and figured by RUEDEMANN and HSÜ, of dichograptid type with dorsal spines" (p. 433). However, the nodes in *T. spinatus* (and also in *T. spiniformis*) are narrow and spine-like, while, distally, the strong curvature of the proximal thecae is reduced or absent.

DISCUSSION.—KOZŁOWSKI (1954) defined the genus *Holmograptus* to include pendent or declined species of *Didymograptus* with thecae far more elaborate than the normal dichograptid type. He selected *Didymograptus callotheca* BULMAN, 1932, as the type species and also attributed *D. cucullus* BULMAN, 1932, to *Holmograptus*. However, the nature of the thecal elaboration differs appreciably in each of these two species.

In *D. cucullus*, the thecae show geniculate curvature such that the free ventral wall is parallel or sub-paralled to the dorsal stipe margin throughout the observed extent of the stipes. Thecal overlap is of the order of 0.5 proximally, decreasing to 0.33 distally. The thecal apertural margin is bounded by a pronounced, raised rim which is continuous with a distinct, genicular list; in profile, the aperture is slightly concave, whilst the plane of the margin is approximately parallel to the dorsal wall of the stipe, and the apertural region can be described as exhibiting incipient extroversion (see BULMAN, 1932*b*, p. 16, fig. 1*b*).

A sub-apertural spine is developed on the free ventral wall, just proximally to the ventral margin of the aperture. This spine is not directly concerned in the form of the apertural margin; however, from the base of the spine to the ventral rim of the aperture, the free ventral wall is inclined distally and dorsally, thus coming into line with the concave form of the apertural margin (see BULMAN, 1932*b*, p. 16, fig. 1*b*). In profile, therefore, the appearance is of a shallowly-concave aperture extending (dorso-ventrally) from the geniculum to the ventral spine (see BULMAN, 1932*b*, p. 16, fig. 1*a*: $th1^1$, $th1^2$ and $th2^2$); in fact, a distinct rim is present some distance beyond the spine, and this is the true proximal margin of the aperture (Figs. 31, 32).

HOLM's plate figures (see BULMAN, 1932*b*, pl. 7 (IV: 1), figs. 1–8) are sometimes inaccurate in their representation of the structure of the thecal aperture in *D. cucullus*; thus, in figs. 1, 3 and 4 the ventral margin is not indicated, and the degree of development of the genicular lists as shown in figs. 7 and 8 is seldom achieved.

The proximal thecae in *D. callotheca*, as in *D. cucullus*, show geniculate curvature, so that the free ventral wall is approximately parallel to the dorsal stipe margin; distally, however, on the basis of the probable identity of *D. callotheca* BULMAN, 1932, with *D. lentus* TÖRNQUIST, 1911, and *Tylograptus geniculiformis* MU, 1957, the thecae are inclined to the dorsal wall at angles of up to 25°, whilst curvature is reduced or absent. Furthermore, whilst overlap is of the order of 0.5 proximally, as in *D. cucullus*, it increases distally to 0.66.

Unlike *D. cucullus*, the mode of growth of the prothecal part of each theca is such as to produce, at the origin of each theca, a distinct node on the dorsal wall of the stipe. Proximally, each node is positioned at a level along the stipe just beyond (i.e. distally to) a thecal aperture (see, for example, BULMAN, 1932*b*, p. 17, fig. 2). Distally, as in the stipe fragment figured by KOZŁOWSKI (1954, p. 433, text fig. 6), the node is situated in front of (i.e. proximally to) a thecal aperture, and in a section normal to the stipe length at the level of the aperture, three thecae are encountered, compared with two proximally. The concavity noted by KOZŁOWSKI, lying below a thecal aperture, and approximately in the position at which a node is developed at the proximal end of the rhabdosome, is simply a result of increased overlap distally along the stipes, combined with the initially looped growth of the prothecae, giving a generally undulating dorsal margin.

The modification of the apertural margin in *D. callotheca* is described below (see p. 43), and here it is sufficient to note that the "flattened disc with slightly raised rim" (BULMAN, 1932*b*, p. 19), present on the ventral wall of the succeeding theca, is not directly concerned with the apertural opening (as is implied in text fig. 3*d*, BULMAN, 1932*b*); the rim (genicular list) surrounding the modified area does not define the distal (dorsal) margin of the thecal aperture. The plane of the apertural margin in *D. callotheca* is normal to the stipe length, and the aperture itself is directed distally; the ventral and lateral edges are modified by a denticle and lappets, respectively, whilst the dorsal edge is entirely free of such structures and is bounded only by a distinct rim (Figs. 49*c*, 50).

In comparison with the present material, some of HOLM's plate figures of *D. callotheca* give a false impression of the morphology of the species. In the diagrammatic dissection of the proximal end (BULMAN, 1936, pl. 2, fig. 4), for example, the implication is that the plate on the ventral wall of the succeeding theca is the distal (dorsal) portion of the thecal aperture and, therefore, that the aperture is extrovert, as in *D. cucullus*; in point of fact, there is no outwardly-curved portion of the interthecal septum, which, on the contrary, terminates at the level along the theca of the origin of the ventral denticle (the plane of the aperture is normal to the stipe length). In this same figure, the course of the proximal end of each septum should be consistent with the curved mode of growth of the corresponding protheca. Finally, $th2^1$ clearly seems to be derived from $th1^2$ and not from $th1^1$ as indicated in the reconstruction.

It is concluded that the thecae of *D. cucullus* and *D. callotheca* are comparable only in that they show geniculate curvature of the free ventral wall; the form of the prothecae and the nature of the apertural modifications are so at variance in the two species as to preclude any close genetic affinity.

MU (1957) has drawn attention to the fact that his genus *Tylograptus* differs from *Holmograptus* only in the more pronounced development of the nodes on the dorsal stipe margin. In particular, he notes that his species *T. geniculiformis*, "in the mode of development and in the elaborated thecae, ... stands nearest to *Holmograptus callotheca* (BULMAN), but differs from the latter in the well developed dorsal folds [nodes] of the thecae" (p. 430). It is suggested below (p. 44) that this latter feature may reflect only the differing mode of preservation of MU's material, and that his species is, in all probability, conspecific with *D. callotheca* BULMAN, 1932.

The thecal aperture in *Tylograptus* is stated by MU to be introverted and introtorted and is sometimes provided with a ventral spine. It is of interest to note that flattening of the aperture of *D. callotheca*, in a dorso-ventral plane, combined with a poor state of preservation, would give the impression of an introverted aperture with ventral spine. Further correspondence between *D. callotheca* and *Tylograptus* includes the strong curvature of the proximal thecae, though it is as yet uncertain whether a geniculum is developed in *Tylograptus* (see JAANUSSON, 1964, and above p. 38). Also, there is evidence in *D. callotheca*, as in *Tylograptus*, of increased overlap distally and the consequent presence of more thecae in a section normal to the stipe length.

An *extensus* stage of proximal end development in *D. callotheca* BULMAN, 1932, seems likely, and the material from the Lower *Didymograptus* Shale at Tossåsen which BULMAN (1950*a*) has attributed to *D. callotheca* also exhibits this stage of development. The mode of proximal end development in *Tylograptus* is unknown and MU's suggestion that the *bifidus* stage is represented is derived from an incorrect interpretation of the mode of development in *D. callotheca* BULMAN, 1932 (see BULMAN, 1936, p. 23).

Thus, it would appear that the type species of the genus *Holmograptus* is most probably conspecific with *Tylograptus geniculiformis* MU and that these differ from other species attributed to the genus *Tylograptus* primarily in the degree of development of the nodes. Moreover, MU himself claims that *D. callotheca* is the progenitor of the tylograptids. The recognition, therefore, of two genera within this lineage would seem unnecessary.

Holmograptus is here redefined to exclude *D. cucullus*, but to include those species attributed to the genus *Tylograptus* MU, 1957, which becomes a junior synonym of *Holmograptus* as herein emended. *D. cucullus* is chosen as the type species of the genus *Aulograptus* gen. nov.

Holmograptus lentus (TÖRNQUIST, 1911)

Figs. 47–50

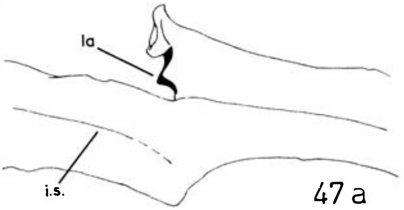
1911 *Didymograptus lentus* n.sp.—TÖRNQUIST, pp. 430–432, pl. 5, figs. 10–15.
1932 *Didymograptus callotheca* BULMAN—BULMAN, pp. 16–19, figs. 2–5.
1936 *Didymograptus callotheca* BULMAN—BULMAN, p. 23, pl. 2, figs. 1–15.
1937 *Didymograptus lentus* TÖRNQUIST—EKSTRÖM, p. 26, pl. 2, figs. 7, 8.
1950 *Didymograptus callotheca* BULMAN—BULMAN, p. 390, figs. 1 *A–C*. [*non* figs. 1 *D–L* = *Maeandrograptus* cf. *leptograptoides* (MONSEN)].
1950 *Didymograptus callotheca* BULMAN—BULMAN, p. 4.
1954 *Holmograptus callotheca* BULMAN—KOZŁOWSKI, pp. 432–34, fig. 6.
1955 *Didymograptus callotheca* BULMAN—BULMAN, p. V80, fig. 57, 1 *d*, *e*.
1957 *Tylograptus geniculiformis* n.sp.—MU, pp. 429–30, text fig. 14*a*, pl. 5, figs. 1, 2, pl. 8, fig. 1.
1960 *Holmograptus lentus* TÖRNQUIST—JAANUSSON, pp. 341, 342, pl. V, fig. 11.

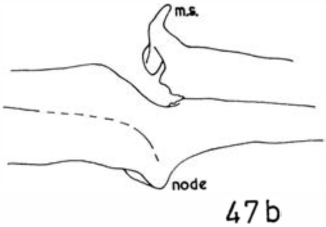
FIGURED MATERIAL.—Spec. Nos: Öl. 1199, Öl. 1200*a*, Öl. 1201.

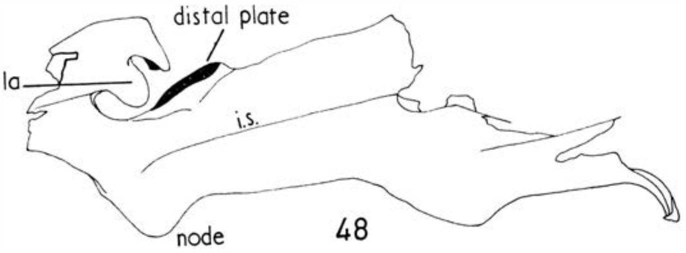
LOCALITY AND HORIZON.—Hälludden: +23 +26 D, +38 +43 D.

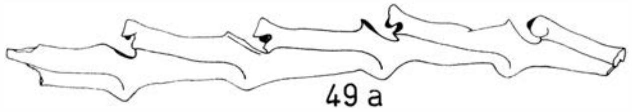
DESCRIPTION.—Only short stipe fragments of this species have been recovered from the present Öland limestones; the longest specimen (Öl. 1201, Fig. 49*a*) has only four thecal apertures preserved.

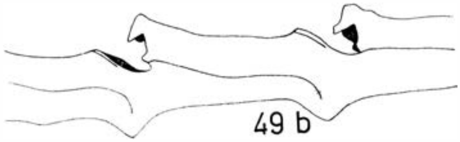
Whilst undoubtedly belonging to the form described by BULMAN (1932*b*) from these same limestones, the present material suggests the development of appreciably fewer thecae per cm, combined with a considerably greater dorsoventral stipe width. Thus, Öl. 1201 (Fig. 49*a*) has four thecae in 4.1 mm of stipe length, suggesting the presence of 9–10 per cm; Öl. 1199 (Fig. 47) has three

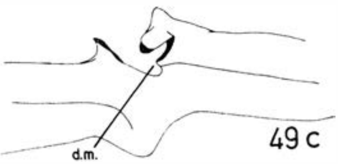


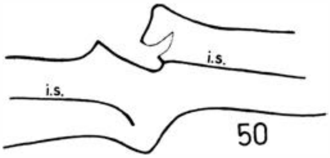












Figs. 47–50: *Holmograptus lentus* (Törnquist, 1911). (47) Stipe fragment; (47*a*) lappets on the apertural margin; (47*b*) median spine on the ventral apertural process. × 35. Hälludden + 38 + 43 D; Öl. 1199. (48) Stipe fragment showing enlarged lappets and lack of median spine on apertural margin. × 35. Hälludden + 23 + 26 D; Öl. 1200*a*. (49) Stipe fragment; (49*a*) complete specimen, × 17; (49*b*) part of same enlarged showing absence of median spine on apertural process, × 26; (49 *c*) same, showing restricted thecal aperture, × 36. Hälludden + 38 + 43 D; Öl. 1201. (50) Diagrammatic longitudinal section of stipe. *d.m.:* dorsal (distal) margin of aperture; *la:* lappet; *i.s.:* interthecal septum; *m.s.:* median spine.

thecae in 3 mm, indicating 10 per cm. Öl. 1201 (Fig. 49*a*) is derived from close to the proximal end of a rhabdosome: at the first aperture preserved, the dorso-ventral width is 0.45 mm, which is increased to 0.62 mm at the level of the fourth. The greatest dorso-ventral stipe width recorded at a thecal aperture is 0.82 mm, in Öl. 1200*a* (Fig. 48).

Detailed differences also exist in the form of the thecal aperture in comparison with the material described by BULMAN (1932*b*). A "knobbed or bifurcated sub-apertural median spine" (1932*b*, p. 19) is stated to be a characteristic feature of the process developed from the ventral margin of the aperture, but in only one instance (Fig. 47*b*) is such a spine prominently displayed in the present material: the almost complete absence of pronounced spines does not seem to favour a preservational explanation for this feature.

The fragments recovered suggest that the thecal aperture in this species is even more restricted than was indicated by BULMAN (1932*b*, fig. 3*d*). Though the difference is slight (see Fig. 50), the effect is significant for, if the present Hälludden material is correctly interpreted, the aperture lies in a vertical plane and is much restricted. The distal (dorsal) margin is not formed by part of the free ventral wall of the succeeding theca, and the structure developed on this wall, resembling a "flattened disc with slightly raised rim" (1932*b*, p. 19), is wholely external to the thecal aperture. The dorsal margin is usually obscured by the ventral process, but it is diagrammatically indicated in Fig. 50, and is seen, for example, in Fig. 49*c*; in some cases, a pair of laterally-positioned lappets is present on the apertural margin of the theca (Fig. 47*a*); typically, the lappets are small and sharply terminated, but in Öl. 1200*a* (Fig. 48) they are rounded and show an exaggerated development.

DISCUSSION.—JAANUSSON (1960) has suggested that *H. callotheca* (BULMAN, 1932) is conspecific with *H. lentus* (TÖRNQUIST, 1911), described from the Upper *Didymograptus* Shale of Fågelsång, in Scania. Such an identity, if correct, is of the utmost importance stratigraphically, since *H. lentus* seems to be confined to the Zone of *D. bifidus* in Sweden (EKSTRÖM, 1937; HEDE, 1951).

The true form of the thecal aperture in TÖRNQUIST's specimens is not known since they are preserved as pyritized internal moulds and "hence a close comparison of all apertural details with those of isolated limestone specimens is not possible" (JAANUSSON, 1960, p. 341). On the other hand, distinct dorsal nodes at the proximal end of the rhabdosome, and interthecal septa originating in those nodes, are clearly evident in *H. lentus* (see TÖRNQUIST, 1911, pl. 5, fig. 14).

In both species, the sicula is sub-cylindrical in form and is abruptly terminated proximally, and there is agreement in the levels and angles at which the first two thecae leave the sicula; further to this, an *extensus* stage of proximal end development is present in each of the two species.

An increase in thecal length and overlap in a distal direction characterises *H. lentus* and *H. callotheca*. The latter species is known largely from near-proximal fragments, but in *H. lentus* the stipes may reach at least 7 cm in length and at this level the width is 0.9 mm, thecal length averages 3.7 mm, overlap is within the range 0.64–0.71 and a section across a stipe at a thecal aperture will pass through four thecae.

The decisive factor in the question of the affinity of *H. lentus* and *H. callotheca* must be the form of the thecal aperture in the former. Apart from this unknown quantity, agreement is noted in respect of the attitude of the stipes, their dimensions, the form of the dorsal stipe margin, the number of thecae developed per cm and the distal increase in thecal overlap. Bearing in mind the uncertainty which must always exist in the comparison of isolated with non-isolated material, the writer would agree that the evidence available supports JAANUSSON's suggestion that *H. callotheca* is, in all probability, a junior synonym of *H. lentus*.

MU (1957) notes that his species *Tylograptus geniculiformis* closely resembles *H. callotheca* (BULMAN, 1932), differing only "in the well developed dorsal folds [nodes] of the thecae" (p. 430). It is not unlikely, however, that the distinction which MU draws between these two species simply reflects their differing modes of preservation: flattened as against isolated and in relief, respectively. Squashing of the rhabdosome in the former could account for the more pronounced nodes, while the form of the apertural process in *H. callotheca* is such that flattening in a dorso-ventral plane would readily give the impression of an introverted aperture such as is stated to be present in *Tylograptus*. Furthermore, the degree of development of the dorsal nodes decreases from the proximal to the distal ends of the stipes in both species and in this respect *T. geniculiformis* differs from other species of *Tylograptus*, in which the nodes are of equal or of increased prominence distally. It is also to be noted that the dimensional details of the distal parts of *H. lentus* compare closely with those of *T. geniculiformis*.

Genus *Maeandrograptus* MOBERG, 1892

TYPE SPECIES.—*Maeandrograptus schmalenseei* MOBERG, 1892.

DIAGNOSIS.—Rhabdosome didymograptid. Prothecal folds developed, giving undulate dorsal stipe margins. Thecae elongate and sigmoidally curved at least proximally; genicular region broadly rounded; apertural margin with rounded lateral lappets and a simple or complex ventral process.

SPECIES.—*Maeandrograptus schmalenseei* MOBERG, 1892.
Didymograptus leptograptoides MONSEN, 1937.
Didymograptus mobergi TÖRNQUIST, 1901.
?*Maeandrograptus* ? *geniculatus* sp. nov.

DISCUSSION.—Much difference of opinion exists in the literature concerning those features of *Maeandrograptus* which can be regarded as generically significant and, particularly, confusion with *Isograptus* is most marked. This stems from the failure of the original diagnoses (MOBERG, 1892) to give any unique characteristics of either genus.

BULMAN (1932*b*) observed that a comparable stage of proximal end development, with th1^2 dicalycal, characterises the type species of both genera, but in *I. gibberulus* the first few thecae grow entirely downwards and the stipes taper distally, while in *M. schmalenseei* the initial thecae are reclined and are noticeably concentrated about the sicula. BULMAN remarked, however, that since so little was known at that time of species of *Isograptus* other than *I. gibberulus* "it is a matter of doubt which characters are of generic significance" (1932*b*, p. 22); and *Maeandrograptus* was then a monotypic genus.

HARRIS (1933) failed to establish a clear-cut distinction between *Isograptus* and *Maeandrograptus*, though it would seem that he regarded stipe attitude as significant, for he noted that "it would be difficult to distinguish between *Isograptus hastatus* and a specimen of *Maeandrograptus tau* with reflexed stipes" (1933, p. 107). Certainly, thecal form, at least at the proximal end of the rhabdosome, bears little or no relation to the generic affinity of the species which he describes; thus, he is unable to decide upon the identity of one proximal end specimen (1933, text fig. 50) as *I. dumosus* or *M. aggestus.*

The diagnoses of *Isograptus* and *Maeandrograptus* given in the Treatise (BULMAN, 1955) emphasize thecal form and the attitude of the proximal thecae. In species of *Isograptus*, the first few thecae are entirely pendent and all the thecae are inclined at a high angle to the dorsal stipe wall, while in *Maeandrograptus* the first theca of each stipe is reclined and all the thecae have a low inclination to the dorsal margin. Rigid application of these diagnoses leaves in doubt the generic affinity of such species as *I. manubriatus* (T. S. HALL), *I. hastatus* HARRIS and *I. dumosus* HARRIS, in each of which the first one or two thecae of each stipe grow downwards, parallel to the sicula, but subsequent proximal thecae are inclined at a low angle to the dorsal stipe margin throughout their length.

I am indebted to Dr. JAANUSSON for drawing my attention to the possibility that the undulations present on the dorsal margins of the stipes of *M. schmalenseei* may be a reflection of prothecal folding comparable with that portrayed by species of *Holmograptus*. The writer has examined specimens of *M. schmalenseei* and clearly this species does have prothecal folds. These are illustrated in the plate figures accompanying BULMAN's (1932*b*) description of this species and, moreover, the interthecal septa are seen to bend at their origins into the folds just as they do in *Holmograptus lentus*. Incidentally, both *M. schmalenseei* and *H. lentus* show a distal increase in thecal length and a distal reduction in thecal overlap and in the degree of development of the dorsal undulations.

On the evidence of prothecal folding, elongate and sigmoidally curved thecae and a reflexed stipe attitude, *Didymograptus mobergi* TÖRNQUIST, 1901, can be attributed to *Maeandrograptus* and it is interesting to record that MOBERG had given this species the manuscript name "*Maeandrograptus angustatus*". A further, detailed correspondence between *M. schmalenseei* and *D. mobergi* lies in the common presence of a thread-like ventral process with expanded termination, which recalls the processes developed in *Dictyonema cotyledon* BULMAN and *Dictyonema peltatum* WIMAN.

Didymograptus leptograptoides MONSEN is included in *Maeandrograptus* by

Jaanusson (1964) in view of the prothecal folding, the sigmoidal thecal shape and the presence of rounded lappets on the apertural margin. It differs from *M. schmalenseei* and *M. mobergi* principally in having narrower stipes, which are declined rather than reflexed, and in lacking elaborate ventral, apertural processes.

A new species from Öland is tentatively placed in *Maeandrograptus*. Unfortunately, in this species, *Maeandrograptus ? geniculatus* sp. nov., a complete rhabdosome is not known, but prothecal folds are developed and distally the thecae have a low inclination. On the other hand, the arrangement of the proximal thecae is more reminiscent of *Isograptus gibberulus*, and the thecae lack a pronounced sigmoid curvature.

Maeandrograptus? geniculatus sp. nov.

Figs. 51–59

Holotype.—No. Öl. 1209; figs. 54 and 56.

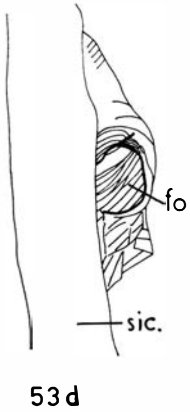
Figured Material.—Nos. Öl. 1206*a*, Öl. 1207–Öl. 1212.

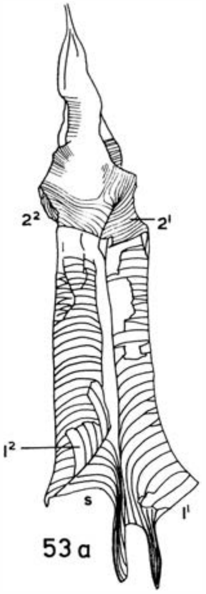
Locality and Horizon.—Hagudden: −83 −86.

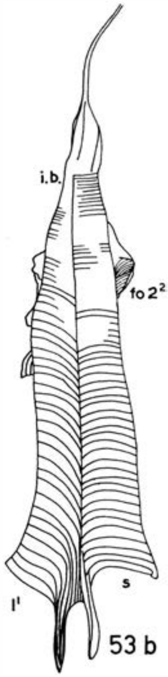
Diagnosis.—Form of complete rhabdosome unknown. Stipes initially horizontal, later reclined; dorsal margin undulate, at least proximally, due to prothecal folding. Sicula long and slender, provided with a prominent denticle. Proximal thecae deflected away from the sicula aperturally; aperture provided with strongly recurved denticle and rounded, lateral lappets; thecae decrease in length distally along stipe and inclined at low angle to dorsal margin; possibly 16 thecae developed in first cm.

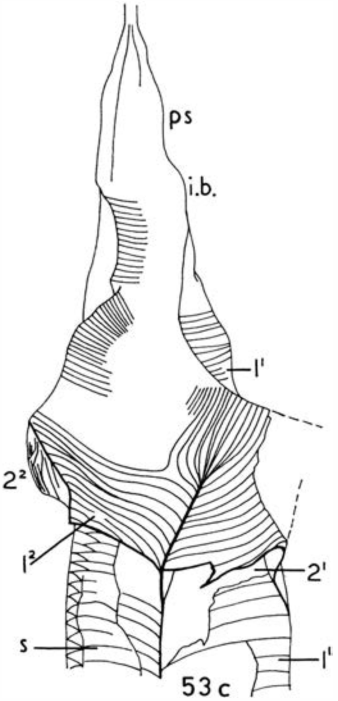
Description.—All the specimens which have been recovered are from the proximal end of the rhabdosome, and all are growth stages; the form of the complete rhabdosome and of the distal thecae are unknown. Initially, the two stipes are horizontal or slightly declined, but a reclined attitude is quickly achieved (Figs. 54*a*, *b*, 55).

The sicula is long (2.7 mm) and slender, averaging 0.40–0.45 mm in width at the aperture. It is straight for the greater part of its length, but is slightly flexed as the aperture is approached. A prominent, broad and roundly-terminated denticle is present on the ventral apertural margin, having a maximum length of 0.5 mm (Figs. 51–53 show stages in its development); in addition, two rounded, laterally-positioned lappets are developed on this margin (Figs. 54 *a*, *b*). A stout nema is produced from the prosicula. This latter is typically short (c. 0.33 mm), compared with the total length of the sicula, and may be parallel-sided or slightly expanding to the distal margin, which is of average diameter 0.12 mm. Occasional longitudinal rods are the only evidence of structure in the prosicula.









Figs. 51–53: *Maeandrograptus ? geniculatus* sp. nov. (51) Immature sicula with initial bud. ×63. Hagudden −83 −86; Öl. 1206*a*. (52) Same, but slightly more advanced. ×35. Hagudden −83 −86; Öl. 1207. (53) Growth stage including foramen of th 2²; (53*a*) reverse aspect, ×25; (53*b*) obverse aspect, ×25; (53*c*) part of reverse side enlarged, ×43; (53*d*) foramen of th 2², ×63. Hagudden −83 −86; Öl. 1208. *fo:* foramen; *i.b.:* initial bud; *ps:* prosicula; *s:* sicula; *v.d.:* ventral denticle.

In general, the proximal thecae decrease in ventral wall length with distance from the sicula. This may be illustrated by the following sets of measurements:

Spec. No. Öl. 1209 (Figs. 54 a, b)

Thecal No.	4^2	3^2	2^2	1^2	sic	1^1	2^1	3^1	4^1
Ventral wall length (mms)	2.2	2.25	2.3	2.7	2.7	2.5	2.3	2.0	2.2
Overlap	c.78	c.7	0.75	—	—	—	0.78	0.78	0.8

Spec. No. Öl. 1210 (Figs. 55)

Thecal No.	7^2	6^2	5^2	4^2	3^2	2^2	1^2	sic
Ventral wall length (mms)	2.0	2.0	2.0	2.2	2.25	2.25	2.4	—
Overlap	—	c.75	c.66	c.78	0.82	c.78	—	—

Overlap is variable, with no marked tendency either to increase or to decrease distally; in all instances, however, the distance for which two adjacent thecae are in contact is a very large proportion of the total ventral wall length of the younger theca.

The proximal thecae typically exhibit a strong flexure—directed away from the sicula—at some point along their length, which is dependent upon their position in the rhabdosome (Figs. 54 *a*, *b*, 55).

The distal decrease in thecal length at the proximal end of the rhabdosome is accompanied by a reduction in dorso-ventral stipe width, as is illustrated by the following measurements:

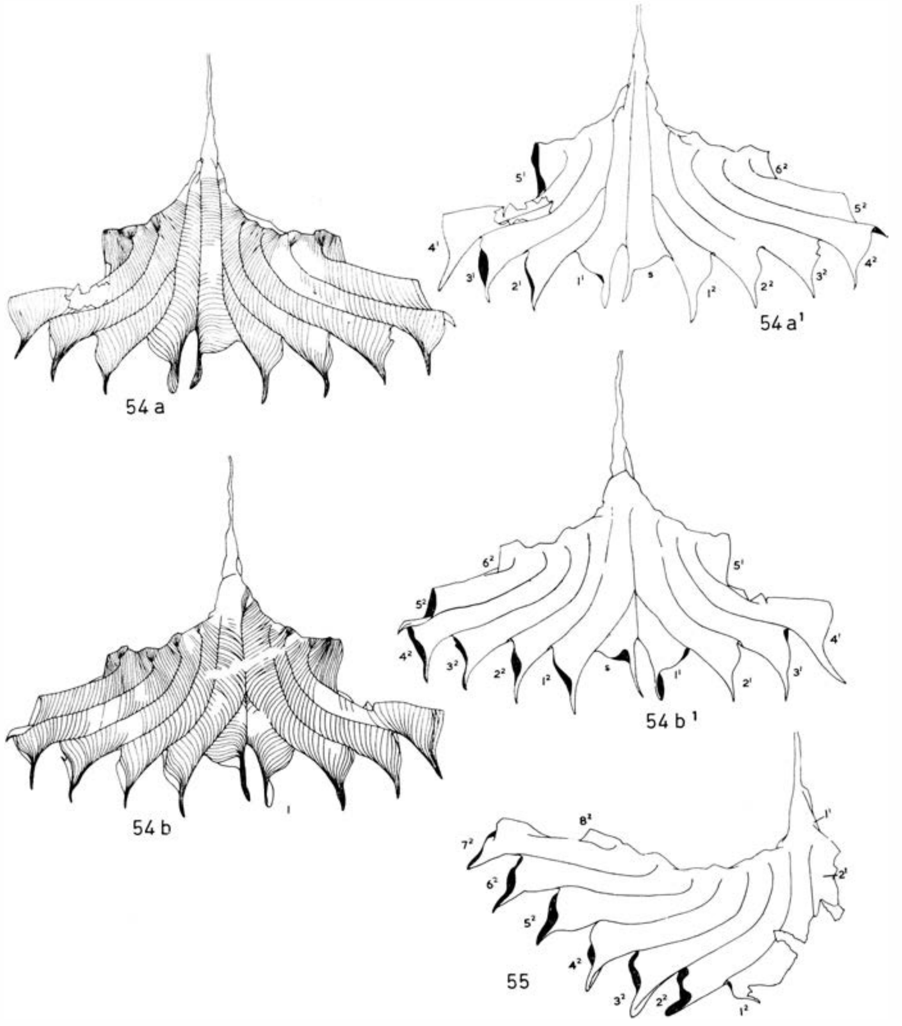
Spec. No. Öl. 1210 (Fig. 55)

Aperture th2^2 to dorsal margin adjacent to th5^2: 1.55 mm
Aperture th4^2 to dorsal margin adjacent to th7^2: 1.50 mm
Aperture th5^2 to dorsal margin adjacent to th8^2: 1.25 mm

A line from the ventral margin of the aperture of th2^2, normal to the dorsal wall of the stipe, cuts five thecae; a similar line from the aperture of th5^2 cuts only four thecae.

In Öl. 1210 (Fig. 55), four thecae are present in 2.5 mm of stipe length, suggesting that 16 thecae per cm may be developed at the proximal end of the rhabdosome.

The thecal apertures reproduce the form of the sicula aperture with only slight modifications: the lateral lappets may be more pronounced, whilst the ventral denticle, though similarly broad and roundly-terminated, may be quite strongly curved, and is always curved to some degree (Figs. 54 *a*, *b*, 55). The lappets are formed not so much by curvature of the fuselli close to the aperture, as by recession of growth at the dorso-lateral margins (see Fig. 56, 57). Th3^2, Fig. 56, has several closely-set, irregular growth lines at the aperture, and the lappets, in consequence, are less obvious. The thecal apertures do not show secondary chitinous thickening of the margin, presumably because all the specimens are growth stages. The dorso-ventral dimension of the thecal aperture is relatively constant, at *c.* 0.4 mm.



Figs. 54–55: *Maeandrograptus ? geniculatus* sp. nov. (54) Holotype; (54*a*) obverse aspect, × 11; (54a^1) same, with thecal numbers, × 11; (54*b*) reverse aspect, × 11; (54b^1) same, with thecal numbers, × 11. Hagudden –83 –86; Öl. 1209. (55) Stipe 2, reverse aspect, × 9. Hagudden –83 –86; Öl. 1210.

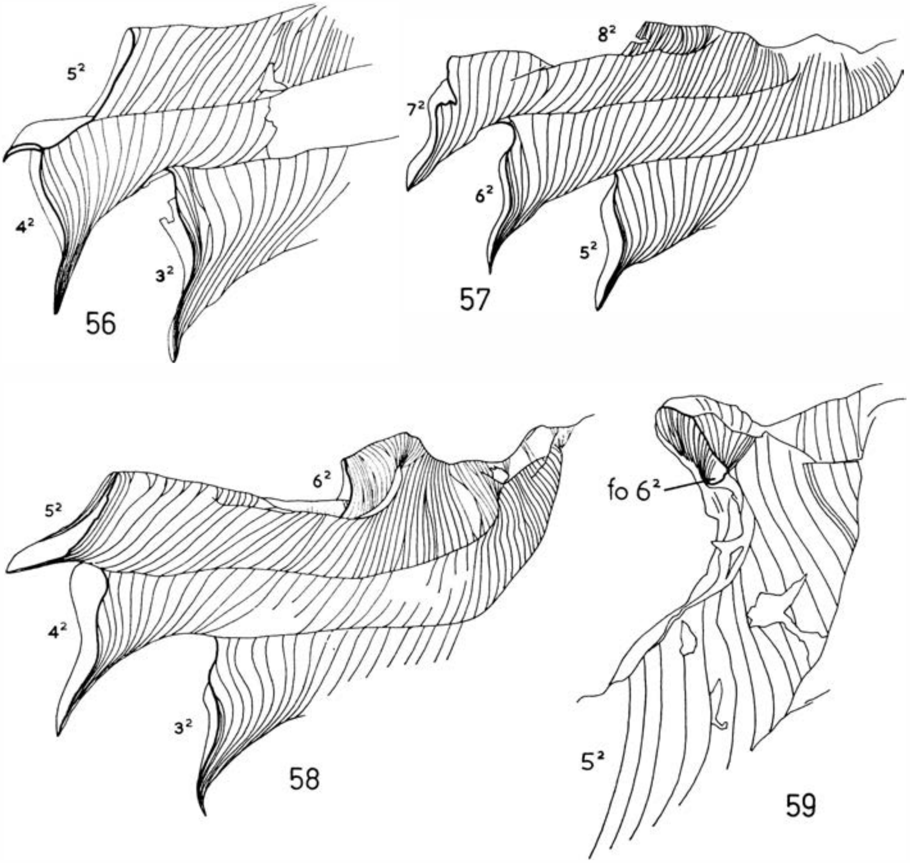
THE INTERTHECAL SEPTA AND RELATED STRUCTURES.—The undulations typically developed on the dorsal margins of the stipes in *M. ? geniculatus* reflect prothecal folding comparable with that present in *Holmograptus lentus*. Details of the courses of the growth lines and of the interthecal septa in these folds are well seen in Figs. 58 and 59.

Figs. 54*a*, *b*, 55, 57 and 58 illustrate very clearly that the growth of the parent theca ('n') is almost completed before the development of the daughter theca ('n + 1') is begun in earnest. If, as in the normal graptoloid condition, th'n + 1' originates in a primary notch, as distinct from a resorption foramen, then once the foramen is formed, either the growth of th'n' must proceed at a phenomenal rate relative to that of th'n + 1', or else the appearance of the latter must be delayed, in order that the growth of the parent theca shall be far in advance of that of the daughter theca, as noted above. The tenuity of the fuselli in the prothecal portion of a theca, in contrast with their development in the metathecal part, would favour the former interpretation: the growth of a theca up to the appearance of the foramen is markedly slow, but thereafter it progresses at a rapid rate. This implies that the interthecal septum, throughout the distance two thecae are in contact, is the dorsal wall of the parent theca, th'n'; observation of the growth lines on the septum in relation to those of the lateral walls of th'n', together with the distal convex arching of the septum, confirms this view.

In Figs. 54*a*, *b*, it will be noted that $th4^2$, in addition to possessing a ventral denticle, seems also to have a dorsal one—but this latter is, in fact, a spatulate or tongue-like process which will become the ventral denticle of $th5^2$. The mode of development of this structure appears to be precisely as described by KOZŁOWSKI (1953) in the case of th1 in his species *Corynoides divnoviensis* (later (1956) transferred by KOZŁOWSKI to his new genus *Corynites*). At the stage of growth reached by $th5^2$ (Fig. 56), the aperture of the theca may be considered as being in two parts: a posterior portion (the actual opening of the theca), which is semi-circular and is bordered by dorsal and lateral walls, and an anterior portion, comprising the tongue-like process. This latter is connected with the main, or posterior, part of the aperture by two ventro-lateral ridges, which, as in *Corynites divnoviensis*, are presumably continuations of the lateral walls of the theca ($th5^2$) where the fuselli have become greatly attenuated and probably, in part, pinched out. These fuselli enlarge again, at some distance from the thecal opening, and unite ventrally to form the tongue-like process —which is the ventral denticle of the thecal aperture (of $th5^2$). This denticle is not formed by a continuation of the ventral wall, as is typically the case in the graptolites, since $th5^2$ lacks such a wall (the 'ventral wall' of $th5^2$ is the interthecal septum separating this theca from $th4^2$—which is the dorsal wall of $th4^2$).

DEVELOPMENT.—The initial bud (Fig. 51) appears on the virgellar side of the sicula, and is developed very high, on the prosicula, about 0.2 mm below the base of the nema. This bud grows downwards parallel to the sicula for a short distance, until a slight embayment is developed in the reverse side of the growing edge; this is the earliest stage in the production of the $th1^2$ foramen; in Fig. 52, this latter foramen is 0.4 mm below the initial foramen.

$Th1^1$ continues the downward direction of growth of the initial bud and lies against the sicula for the greater part of its length, diverging only as the sicula aperture is approached (Figs. 53*a*, *b*, 54*a*, *b*). The development of $th1^2$ follows very quickly after the appearance of the initial bud; the course of this theca is such as to completely obscure the sicula on the reverse side, except for its proximal and apertural extremities. The sicula aperture is exposed because of



Figs. 56–59: *Maeandrograptus ? geniculatus* sp. nov. (56) Holotype: growing tip of stipe 2. × 35. Hagudden − 83 − 86; Öl. 1209. (57) Growing tip of stipe 2. × 26. Hagudden − 83 − 86; Öl. 1210. (58) Growing tip of stipe 2. × 35. Hagudden − 83 − 86; Öl. 1211. (59) Growing tip of stipe 2 with foramen of th 6^2. × 85. Hagudden − 83 − 86; Öl. 1212. *fo*6^2*:* foramen of th 6^2; *s:* sicula.

pronounced curvature affecting the distal portion of th1^2, directing its aperture away from the sicula (Figs. 54*a*, *b*). Th1^2 is dicalycal and gives rise to th2^1 and th2^2 at approximately the same level, as in the *hirundo* stage of proximal end development (see BULMAN, 1936, text fig. 25*f*).

The interthecal septum separating th1^2 and th2^1 is at first directed away from the sicula; at its inception, therefore, th2^1 grows outwards, approximately normal to the length of the sicula, but it very soon changes direction to grow down, parallel to the sicula, along the reverse wall of th1^1. As in the case of the sicula, th1^1 is, in consequence, obscured on the reverse side, except proximally and aperturally, where curvature of th2^1 exposes the aperture of th1^1 (Fig. 54*b*).

Th2^2 is given off from th1^2 at about the same level as th2^1, but on the opposite side of the sicula (Figs. 53*a*, *c*). The initial part of the th2^2 is not clearly preserved in any specimen, although its foramen is seen in Fig. 53 *d*; the growth of this theca is parallel to the sicula and the early part of th1^2, but aperturally it follows the direction of curvature of th1^2 and accentuates it, so that the aperture is turned away from the sicula at an angle of 45°–50°.

Following the appearance of th2^1 and th2^2, the growth of each stipe proceeds independently, each theca budding off from the preceding one shortly after the origin of the latter. It is worthy of note that the growth of the sicula is quite a lengthy process, and it has been observed to be still incomplete when both th3^1 and th3^2 have appeared.

Discussion.—This species differs from *M. schmalenseei* in the relatively slight degree of deflection away from the sicula of the apertural part of the first theca of each stipe and in an apparent reduction of thecal length distally along the stipes.

The prothecal folding readily distinguishes *M. ? geniculatus* from a number of otherwise closely similar species at present included in *Isograptus: I. manubriatus*, *I. dumosus* and *I. hastatus*.

Derivatio Nominis.—The specific name proposed has reference to the flexure developed in the early thecae.

Family *Corynoididae* Ruedemann, 1908

Discussion.—The apparently isolated position of the Corynoididae (represented by the two genera *Corynoides* Nicholson and *Corynites* Kozłowski) within the Graptoloidea has been discussed by several authorities, notably Bulman (1938, 1944–47), Strachan (1949), Kozłowski (1953) and Jaanusson (1960). It is not now considered that there is sufficient evidence for placing the Corynoididae in a separate order, equal in rank to the Graptoloidea, as was suggested by Hopkinson & Lapworth (1875), though Jaanusson (1960, p. 307) believes that "the morphological discontinuity between Corynoididae and the other graptoloids is so sharp that the inclusion of this family in a separate sub-order, Corynoidina, seems to be well justified".

Kozłowski (1953) has emphasized that the Corynoididae—in common with the early graptoloids—portray some characteristics of the order Dendroidea, and these he considers to be a heritage from the earlier dendroids. Bulman (1938, 1944) and Strachan (1949) have both stressed a resemblance between *Corynoides* and the proximal part of *Isograptus gibberulus* as described and illustrated by Bulman (1932*b*), the suggestion being that the rhabdosomal form of *Corynoides* may be the result of the arrested development of such an isograptid at an early stage in its astogeny.

Before discussing further the affinities of the Corynoididae it is necessary to list those features which may be considered characteristic of the family; these are as follows:

(i) The presence of only two (*Corynites*) or three (*Corynoides*) thecae in addition to the sicula; the last theca (th'x' of KOZŁOWSKI, 1953) is rudimentary.

(ii) Broad, lamelliform processes are present on the apertural margins of the sicula and the fully developed thecae; they may be identical in form in the two cases (*Corynoides*), or they may differ somewhat (*Corynites*).

(iii) The sicula and fully developed thecae are of exceptional length.

(iv) The prosicula accounts for only a very small proportion of the total length of the sicula.

(v) The first theca originates in the prosicula; subsequent thecae arise close to the apical end of the sicula and alternate in origin.

(vi) The thecae, other than the rudimentary one (th'x'), lie against the reverse wall of the sicula and diverge from it only aperturally.

Now, in the form and mode of development of the proximal end, it is clear that *Maeandrograptus ? geniculatus* has many features in common with the Corynoididae. There is complete agreement in respect of points (iii) and (iv) as listed above, while even more striking resemblances are revealed in a comparison of *M. ? geniculatus* with those species of *Corynoides* and *Corynites* whose structure is known in an equivalent amount of detail.

BULMAN (1944–47), in the species of *Corynoides* which he described from the Caradocian limestones of the Laggan Burn, states that each theca originates in a resorption foramen—a feature quite at variance with the structure of normal graptoloids. KOZŁOWSKI (1953), on the other hand, notes that in *Corynites divnoviensis* the first theca arises from such a foramen, but the second, and last, theca (th'x') develops from a primary notch; furthermore, he believes that in the species described by BULMAN (1944–47), thecae subsequent to the first-formed also originate in primary notches. The mode of origin of the thecae in *Corynoides* would thus appear to follow the normal graptoloid pattern.

The detailed structure of the prosicula in the Corynoididae is in some doubt. BULMAN (1944) notes that in *Corynoides* cf. *C. curtus*, for example, "the prosicula shows traces of the spiral line, but little indication of the longitudinal strengthening fibres which are usually the more conspicuous feature of the graptolite prosicula" (p. 25). Again, in the case of *C.* cf. *C. gracilis*, it is stated that "the longitudinal strengthening fibres are not usually visible at all, but their presence is proved by the specimen shown in text fig. 39E, where apically the thin wall of the prosicula has been lost in maceration and the nema is only connected to the sicula by two of these longitudinal fibres" (1947, p. 73). *Corynites divnoviensis* lacks any trace of longitudinal rods in the prosicula and KOZŁOWSKI prefers to interpret those recorded by BULMAN, in *Corynoides* cf. *C. gracilis*, as strips of periderm which have resisted maceration, the periderm being relatively thick close to the base of the nema. The absence of longitudinal rods is a primitive characteristic of the Dendroidea which persists, in all probability, in some of the earliest graptoloids. The lack of such rods in the Corynoididae, on the other hand, may reflect a high degree of specialization, as does the rhabdosome itself.

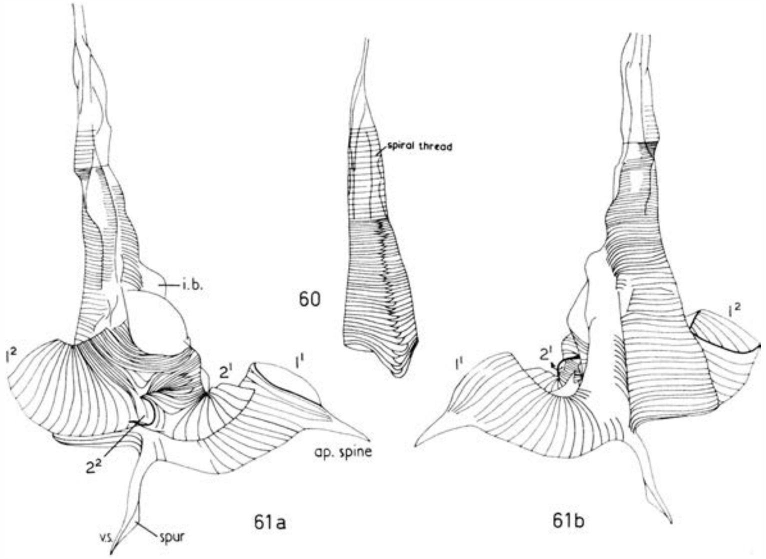
In *Corynoides* cf. *C. gracilis*, *C.* cf. *C. curtus* and *C.* cf. *C. calicularis*, the lamelliform process developed on the apertural margin of the sicula is more or less identical in appearance with the apertural processes developed on the thecae (other than th'x'). In *Corynites*, however, the form of the sicula aperture is strikingly different from that of the single, fully developed theca (see Kozłowski, 1953 and 1956); furthermore, Kozłowski has demonstrated that, whereas the sicular process can be regarded as an extension of the ventral wall of the sicula, the thecal process has quite a different origin, since the first theca (th'a' of Kozłowski, 1953) does not have a ventral wall. In *M. ? geniculatus*, the sicular and thecal processes, whilst approximately identical in appearance are differently produced and in the same manner as in *Corynites*; also, it would seem that in those species described by Bulman, the sicular and thecal processes likewise have a distinct mode of formation whilst remaining similar in appearance. That this is the case is concluded from the description of *Corynoides* cf. *C. gracilis*, in which it is noted that the process on the first theca is produced far in advance of the growing edge of that theca—which is precisely the situation existing during the development of the thecal process in *Corynites* and in *M. ? geniculatus*.

Thus, a comparison of the structure and development of species of *Corynoides* and *Corynites* with *Maeandrograptus ? geniculatus* reveals many remarkable similarities and only a single serious discrepancy: the presence of a dendroid type of prosicula in the former compared with a typically graptoloid one in the latter. On balance, the morphological evidence seems to favour derivation of the Corynoididae from a true graptoloid, such as *M. ? geniculatus*, though this latter could not have been a direct ancestor since it appears to be restricted to the *hirundo* Zone while the Corynoididae is first represented only in the *gracilis* Zone. There would seem to be good reason for recognizing a family Corynoididae as at present defined, but insufficient evidence for establishing a taxon of higher rank to accommodate this one family.

Family *Diplograptidae* LAPWORTH, 1873

Genus *Glyptograptus* LAPWORTH, 1873

Remarks.—In a comprehensive review of *Glyptograptus dentatus* and allied species, Bulman (1963) has commented upon features illustrated by relevant material in the writer's collection from Öland and has attributed this material to *G. dentatus* and *G. austrodentatus* var. *oelandicus*. Full synonymies and descriptions of these forms are given in the work cited above (Bulman, 1963, pp. 673–75 and 682–83) and, with special reference to Öland, in Part 7 of Bulman's monograph on the Holm collection (Bulman, 1936). It seems unnecessary, therefore, to give here a full description of the present Öland glypto-



Figs. 60–61: *Glyptograptus dentatus* (BRONGNIART, 1828). (60) Immature sicula with details of structure of prosicula. × 57. Hälludden + 18 + 22D; Öl. 1223. (61) Growth stage with foramen of th 2^2; (61*a*) reverse aspect, × 44; (61*b*) obsverse aspect, × 44. Hälludden + 18 + 22D; Öl. 1228. *i.b.*: initial bud; *v.s.*: virgella spine.

graptid material and the following account deals only with the characteristics of selected specimens.

Glyptograptus dentatus (BRONGNIART, 1828)

Figs. 60–62

1936 *Glyptograptus dentatus-teretiusculus* transient BULMAN—BULMAN, p. 57, pl. 3, figs. 1–4, 8–11, pl. 4, figs. 1–3.

1960 *Glyptograptus* aff. *teretiusculus* (HISINGER)—JAANUSSON, pp. 341, 342.

1963 *Glyptograptus dentatus* (BRONGNIART)—BULMAN, p. 673, text figs. 1, 4, pl. 96, figs. 1–5. (With full synonymy.)

FIGURED MATERIAL.—Nos. Öl. 1223, Öl. 1228, Öl. 1232.

LOCALITY AND HORIZON.—Hälludden: + 18 + 22D, + 23 + 26D; Hagudden: 0 + 15D, + 10 + 15D.

DESCRIPTION.—The width of the rhabdosome at the level of th1^1 is within the range 1.0–1.2 mm; at th5^1 in Öl. 1232 (Fig. 62*a*) the width is 1.45 mm; and 1.85 mm is the maximum width recorded in any fragment. At the proximal end of Öl. 1232, 4 thecae are developed in 2.75 mm; a distal fragment (Öl. 1233) has 12 thecae per cm.

The glyptograptid thecal form is especially well portrayed in Öl. 1232 (Fig. 62 *a*) and has been described by BULMAN (1963, p. 675). The sigmoidal curvature of the ventral wall of the metatheca is most pronounced proximally and becomes somewhat reduced distally.

In *G. dentatus*, there is incomplete development of the interthecal septum between two adjacent thecae. This is well illustrated in Öl. 1232 (Fig. 62*b*) where it can be seen that the whole of the internal separating wall between th5^1 and th6^1, for example, apart from the lateral edges, is occupied by the foramen of th6^1, the plane of which lies at a very slight angle to the axis of the rhabdosome. A complete septum is produced only at, or just below, the aperture of th5^1, where, strictly, it is not a septum but the free ventral wall. The lateral developments of the septum are indicated externally on the lateral walls of the rhabdosome and show a proximal overlap of less than one-half.

DEVELOPMENT.—The mode of development in *G. dentatus* has been fully described elsewhere (BULMAN, 1963) and here it is intended only to comment upon the features of a number of cleared growth stages which occur in the present Öland material.

The sicula is 1.2–1.3 mm in length and expands to the aperture where it averages 0.30 mm in width. The prosicula portion (Fig. 60) is 0.3–0.4 mm long and 0.1 mm wide at the distal margin; usually, at least four longitudinal primary rods and five or more secondary rods are developed, together with the helicoidal thread. Apart from the virgella spine, which may project for up to 1.1 mm, the margin of the sicula aperture is unornamented. An early stage in the development of the virgella is shown in Öl. 1223 (Fig. 60).

The origins of the first four thecae are contained in Öl. 1228 (Fig. 61). The initial bud appears just within the lower half of the sicula, but in the upper half of the metasicula. The course of th1^1 and the spine on the aperture of this theca are clearly shown. The foramen of th1^2 is not evident, but the initial course of this theca—obliquely downwards towards the sicula aperture and then upwards —can be traced. Th2^1 has only slight downward growth and very quickly turns upwards to occupy the space enclosed by the proximal and distal portions of th1^1. Only the first two or three fuselli of th2^2 are shown, but these are sufficient to indicate that this theca has no downwardly growing portion.

Subsequent development of the proximal end is shown by the advanced growth stage Öl. 1232 (Fig. 62). In particular, the dicalycal nature of th2^2 is well demonstrated in the pattern of the growth lines.

Glyptograptus austrodentatus HARRIS & KEBLE, 1932

REMARKS.—In his review of the early glyptograptids (1963), BULMAN recognized variation amongst material attributable to *G. austrodentatus* of sufficient degree to merit subdivision below the species level, and accordingly he established a number of new varieties of *G. austrodentatus* (1963, pp. 678 ff.). The International Code of Zoological Nomenclature (1961), however, stipulates that, after 1960, a new name proposed explicitly as that of a variety is not available (Art. 15) and is to be regarded as of infrasubspecific rank (Art. 45, e, ii), but such a name can become available if the taxon in question is given a

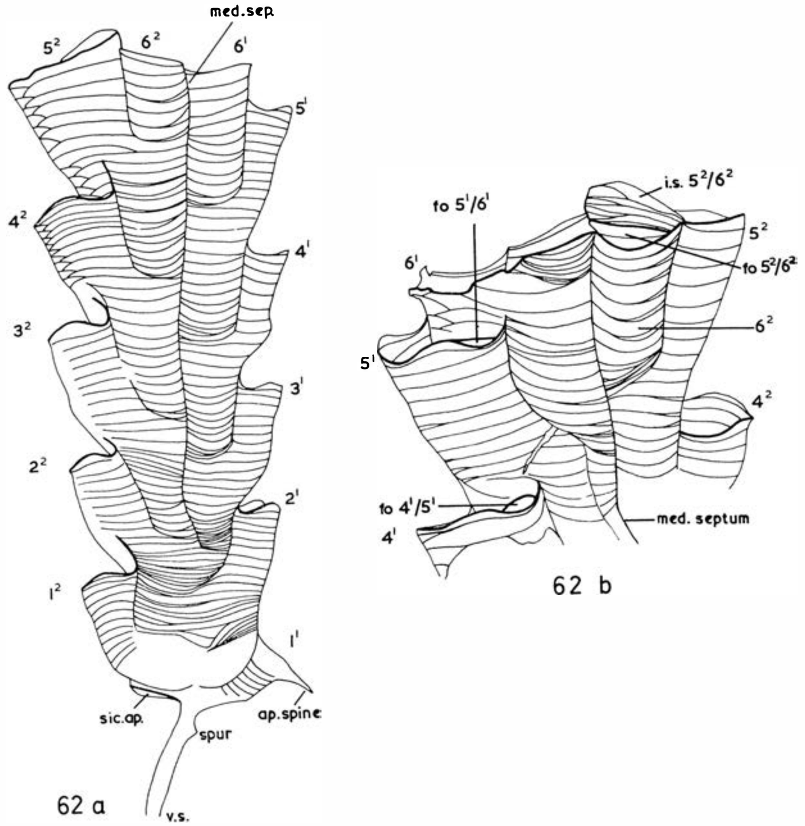


Fig. 62: *Glyptograptus dentatus* (Brongniart, 1828). (62) Advanced proximal end growth stage; (62*a*) complete specimen in reverse aspect, × 25; (62*b*) detail of growing end in obverse aspect, × 35. Hälludden +18+22D; Öl. 1232. *ap:* aperture; *fo:* foramen; *i.s.:* interthecal septum.

rank within the species-group (Art. 10, b). Of the several varieties proposed by Bulman, the writers' immediate concern is with *G. austrodentatus* var. *oelandicus*, and this variety is herein raised to the status of subspecies in order to bring it within the scope of the International Code. A further requirement of the Code is that a taxon so elevated shall take the date and authorship of its elevation (Art. 10, b). In the present case, however, it must be emphasized that the original diagnosis (Bulman, 1963, p. 682) remains unchanged; consequently, it seems advisable to retain Bulman's name in addition to making reference to the present publication. Thus, in future publications, this subspecies can appear as *Glyptograptus austrodentatus oelandicus* Bulman, *in* Skevington, 1965.

Professor Bulman, in correspondence with the writer, stresses that, in palaeontology, one cannot use the term subspecies in any precise zoological sense: his varieties *may* be essentially geographical races (see also Bulman, 1963,

Table 1. Rhabdosomal width at given levels in *Glyptograptus a. oelandicus*, in mm.

Spec. No.	2^1–2^2	4^1–4^2	6^1–6^2	Width at last pair of thecae
395	0.9	1.1	1.25	1.45 (6^1–6^2)
399	0.9	1.15	1.25	1.3 (9^1–9^2)
394	1.0	1.15	1.35	1.35 (7^1–7^2)
493	1.05	1.1	—	1.1 (4^1–4^2)
1647	1.05	1.3	—	1.3 (4^1–4^2)
1649	1.05	1.3	—	1.3 (4^1–4^2)
488	1.1	—	1.45	1.45 (6^1–6^2)
498	1.1	1.2	1.35	1.4 (9^1–9^2)
307	1.15	1.3	1.35	1.45 (8^1–8^2)
Öl. 1230	1.5	1.6	—	1.8 (5^1–5^2)

p. 679), and hence be of true subspecific status, but of this there can be no proof. "Variety" seems a convenient and sufficiently non-committal term to apply in such circumstances.

Glyptograptus austrodentatus oelandicus BULMAN **subsp. nov.**

Figs. 63–65

1936 *Glyptograptus dentatus* (BRONGNIART)—BULMAN, pp. 49–57, text figs. 18–21, pl. 3, figs. 5–7, 12–21, pl. 4, figs. 4–6.

1963 *Glyptograptus austrodentatus* var. *oelandicus* n.var.—BULMAN, pp. 682–683, text figs. 2*a–d*, 8, pl. 97, figs. 16, 17. [*Nomen nudum.*]

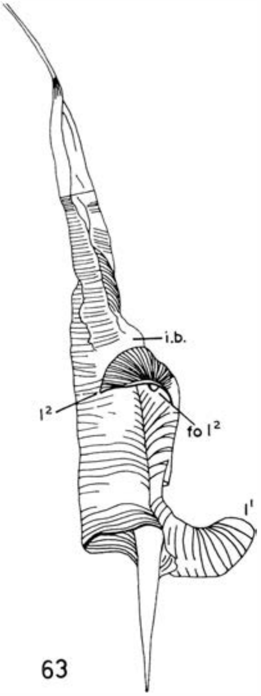
HOLOTYPE.—See BULMAN, 1963, p. 682.

FIGURED MATERIAL.—Nos. Öl. 1227, Öl. 1229, Öl. 1230.

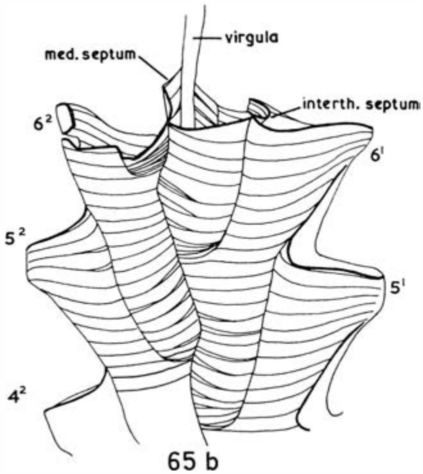
LOCALITY AND HORIZON.—Hälludden: −118 −120D, −113 −116D, −110 −113D, −100D, +5 +8D, +18 +22D, +23 +26D; Hagudden: +20 +45D.

DIAGNOSIS.—See BULMAN, 1963, p. 682.

DESCRIPTION.—The original description of this subspecies, based on material in the HOLM collection, commented on the existence of broad and narrow rhabdosomes (BULMAN, 1936, p. 52). The writer has had an opportunity to re-measure HOLM's material but has failed to verify any such dichotomy, and reference to Table 1 shows that specimens 307 and 394, which were quoted as typical of the broad and narrow forms, respectively, compare closely in dimensions at corresponding levels of the rhabdosome. On the other hand, specimen Öl. 1230 in the writers' collection (figured herein as Fig. 65*a*) is appreciably broader than any of HOLM's specimens but otherwise agrees closely with these latter. Thus, it appears that both broad and narrow forms do exist in this subspecies, with the former apparently less common than the latter, though at present it is not possible to assign any significance to this observation.

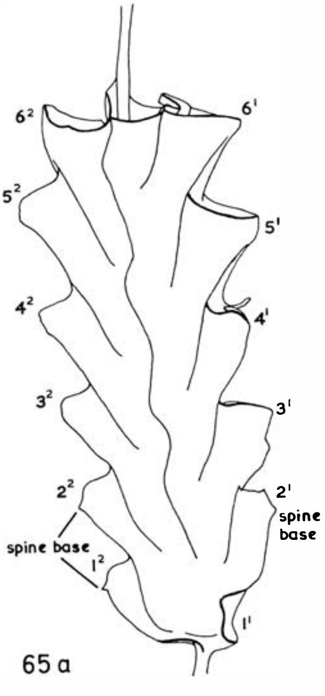


63



65 b

64



65 a

Figs. 63–65: *Glyptograptus austrodentatus oelandicus* BULMAN subsp. nov. (63) Growth stage with foramen of th 1^2. × 35. Hälludden – 118 – 120D; Öl. 1227. (64) Distal part of rhabdosome showing thecal form. × 17. Hälludden – 113 – 116 D; Öl. 1229. (65) Advanced proximal end growth stage; (65 *a*) complete specimen in reverse aspect, × 17; (65 *b*) detail of growing edge in reverse aspect, × 28. Hälludden – 110 – 113 D; Öl. 1230. *fo* 1^2*:* foramen of th 1^2; *i.b.:* initial bud.

The thecal form is well shown in specimen Öl. 1230 (Fig. 65*b*). Curvature of the free ventral wall is sufficiently pronounced to give an incipient geniculum and to cause the supragenicular portion of the wall to lie parallel to the length of the rhabdosome; the length of the supragenicular wall is variable (compare Figs. 64 and 65*b*). The apertural margin is straight or very slightly undulating. A sub-apertural spine is borne on th1^1 and in specimen Öl. 1230 (Fig. 65*a*) spine bases are preserved on th1^2, th2^1 and th2^2.

As in *G. dentatus*, a complete interthecal septum between two adjacent thecae need not be developed, and if one is present it is extremely short. The markedly undulating form of the median septum in this subspecies is well shown in Fig. 65*a*.

DEVELOPMENT.—Only a single early growth stage can confidently be accorded to *G. austrodentatus oelandicus*. In this specimen (Öl. 1227, Fig. 63), th1^1 is almost complete and the foramen of th1^2 has appeared.

The sicula is 1.7 mm in length and 0.29 mm wide at the aperture; the latter is provided with a virgella spine 0.5 mm long. The prosicula portion is 0.4 mm in length; no structural details are evident. The initial bud originates fractionally within the lower half of the sicula. The growth of th1^1 is not quite completed in the specimen. The foramen of th1^2 follows quickly upon the appearance of the initial bud and the first few fuselli of th1^2 are preserved to show clearly the initial upward growth quickly followed by a complete reversal in direction, towards the sicula aperture.

In the advanced growth stage Öl. 1230 (Fig. 65*b*), the growing tip has cleared and shows that, although the stipes are independent at that level (th6^1–6^2), growth proceeds at the same rate on either side of the median septum. The virgula is well in advance of the septum and the growing edge of this latter is arched up on either side towards the virgula, so that the growth lines slope proximally and laterally.

Genus *Pseudoclimacograptus* PŘIBYL, 1947

Pseudoclimacograptus camptochilus sp. nov.

Figs. 66–67

1936 *Amplexograptus* aff. *coelatus* (LAPWORTH)—BULMAN, pp. 61–63, pl. 3, figs. 22, 25–33; ?pl. 3, figs. 23, 24.
1938 *Amplexograptus* cf. *coelatus* (LAPWORTH)—BULMAN, fig. 19*k*.
1955 *Amplexograptus* cf. *coelatus* (LAPWORTH)—BULMAN, fig. 31:8.

HOLOTYPE.—Spec. No. 485, HOLM Collection, Paleozool. Avd., Riksmuseet; figured herein as Fig. 67.

TYPE STRATUM AND LOCALITY.—Glauconithaltig, grå Vaginatumkalk, Hälludden, Öland, Sweden.

DIAGNOSIS.—Width of rhabdosome 0.7–0.8 mm at th1^1–th1^2, increasing gradually to a maximum of 1.5 mm; 7–7½ thecae in 5 mm proximally and 6 in

Table 2. Dimensional details of *Pseudoclimacograptus camptochilus* sp. nov., in mm.

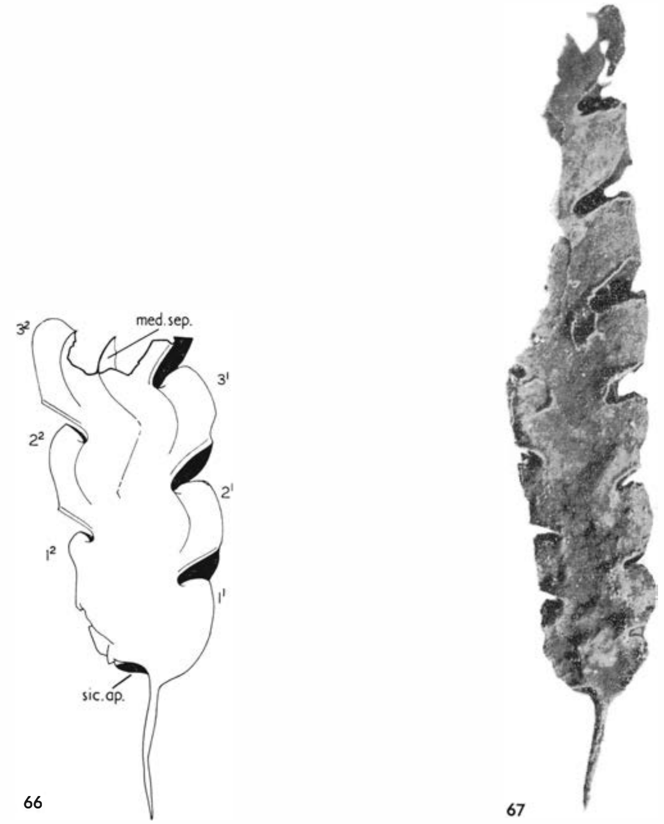
Spec. No.	Width of rhabdosome				Thecal number		Remarks
	1^1–1^2	3^1–3^2	5^1–5^2	maxi-mum	Per 5 mm	First 5 th. excl. 1^1, 1^2 occur in:	
298	0.7	0.8	0.95	0.95 (5^1–5^2)	—	3.1	Prox. fragment
299	—	—	—	1.45	6	—	Dist. fragment
300	—	—	—	1.40	6½–7½	—	Near-proximal fragment
484	0.8	—	—	—	—	—	Prox. fragment
485	0.8	1.0	—	—	7	3.5	Prox. fragment; holotype
1269	—	—	—	1.4	6–6½	—	Dist. fragment
1318	0.7	—	—	—	—	—	Proximal end growth stage
Öl 1236	0.8	0.95	—	—	—	—	Proximal end growth stage

5 mm distally; overlap 0.4 distally. Convex curvature of supragenicular wall strong proximally but somewhat reduced distally. Apertural excavations parallel-sided and inclined, occupying 0.50 the width of the rhabdosome and 0.33 the length of the ventral margin; strong sub-apertural list developed distally. Distally directed parts of th1^1 and th1^2 of exceptional length. Development apparently of streptoblastic type (BULMAN, 1963).

DESCRIPTION.—This species was fully described and illustrated by BULMAN (1936) as *Amplexograptus* aff. *coelatus* (LAPWORTH) from material in the HOLM Collection, but for the sake of completeness the dimensional details of this material are summarised below in Table 2. In addition, an account is given of specimen Öl. 1236 in the present collection from Öland, together with some general comments on the species.

Specimen Öl. 1236 from Hagudden (Fig. 66) is a growth stage with six thecae complete; the specimen has partially cleared but details of the proximal end are not discernible though the thecal arrangement would seem to indicate the streptoblastic type of development (BULMAN, 1963, p. 671). The sicula extends at least as high as the aperture of th2^2, giving a minimum length of 1.4 mm. The distally directed parts of th1^1 and th1^2 are of exceptional length, extending 0.5 mm and 0.8 mm, respectively, above the level of the sicula aperture, and the proximal end has a distinctly tapered outline (see also BULMAN, 1936, pl. 3, figs. 22, 25 and 26).

In Öl. 1236, the geniculum is developed as a narrow list and above this level the supragenicular wall is strongly convex and the thecal aperture distinctly



Figs. 66–67: ***Pseudoclimacograptus camptochilus*** sp. nov. (66) Proximal end of rhabdosome in reverse aspect. ×24. Hagudden 0+15D; Öl. 1236. (67) Holotype in reverse aspect. ×16. Hälludden, horizon not known; No. 485, HOLM Collection.

introverted; at this stage, no sub-apertural list is developed. Distally, however, the curvature of the supragenicular wall is somewhat reduced and a sub-apertural list makes its appearance. In the holotype (spec. 485, Fig. 67), this list is first apparent on $th3^1$ and is fully developed on $th6^1$, and this specimen has been selected as holotype because it illustrates these changes quite well, though in other respects it is poorly preserved.

The zig-zag median septum is clearly in evidence at the growing end of Öl. 1236 (Fig. 66) but is only vaguely indicated on the lateral walls of the rhabdosome, owing to peridermal wrinkling. Some of HOLM's figures (see, for example, BULMAN, 1963, pl. 3, figs. 29 and 30) do not accurately portray the extent to which the median septum is folded along the lateral walls of the rhabdosome in this species, nor do they show the very short transverse lists which are present, though these latter are frequently obscured by wrinkling and by a very thick cortical layer in the distal fragments.

Specimen 1286 in the HOLM Collection (see BULMAN, 1936, pl. 3, figs. 23 and

24) is probably not conspecific with the present species. This suggestion is based on the parallel-sided rather than tapered outline of the proximal end, the only slight convexity of the supragenicular walls and the relative shortness of the distal portions of th1^1 and th1^2.

Discussion.—The convex curvature of the supragenicular walls of the thecae and the zig-zag form of the median septum indicate that this species belongs in *Pseudoclimacograptus* rather than in *Amplexograptus.*

P. camptochilus is distinguished from other species of *Pseudoclimacograptus* principally by the features of the distal thecae, which, however, may be difficult to distinguish in certain types of preservation. The present species seems to be very close to *P. formosus* Mu & Lee, especially in the form of the proximal end, but the latter is preserved as pyritised internal moulds so that it is not possible to compare all details of the thecae. The Chinese species is somewhat narrower and has slightly fewer thecae per unit length; also, in the distal thecae, the geniculation is not so pronounced as in *P. camptochilus* and thecal overlap is greater.

From *P. romanovskyi* Keller and *P. cumbrensis* Bulman, the Öland species differs most noticeably in width of rhabdosome, it being much more slender than either of the two former species.

Occurrence.—Hälludden: −118 −120D, +5 +8D; Hagudden: 0 +15D, +20 +45D.

Derivatio Nominis.—The specific name, *camptochilus*, has reference to the strongly inflected apertural margin in the more distal thecae.

Graptolithina Incertae Sedis

Group *Graptovermida* Kozłowski, 1948

?Graptovermid sp. gen. et sp. indet.

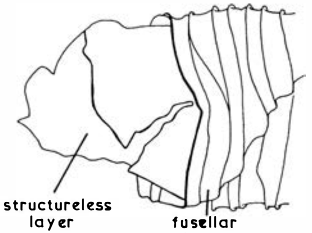
Figs. 68–72

Figured Material.—Nos: Öl. 1237*c*, Öl. 1238*b*, Öl. 1239*a*, *b*, Öl. 1240*d*.

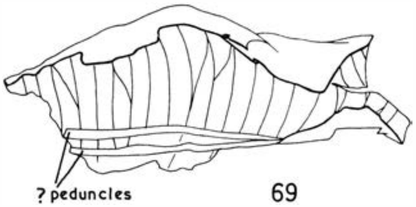
Locality and Horizon.—Hälludden: −118 −120D, −100D, +18 +22D, +23 +26D; Hagudden: 0 −8D, +20 +45D.

Description.—A number of short, robust 'tubes' have been recovered from several levels within the Ontikan limestones of Öland; they are usually squashed to varying degrees, but presumably were originally cylindrical. The longest is 2.5 mm in length; they may be straight or slightly curved and are never branching. The diameter varies from 0.20–0.58 mm, though it is possible that squashing accounts for some of the variation observed; even so, in apparently undeformed specimens, a range in diameter of from 0.20–0.37 mm has been recorded.

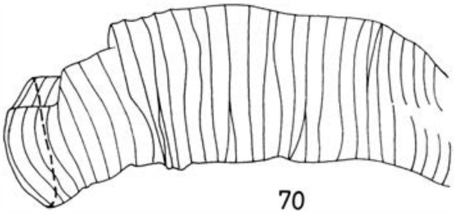
With a single exception − Öl. 1238*b* (Fig. 69), described below—no internal structure is preserved. The walls are composed of two distinct layers: an inner,

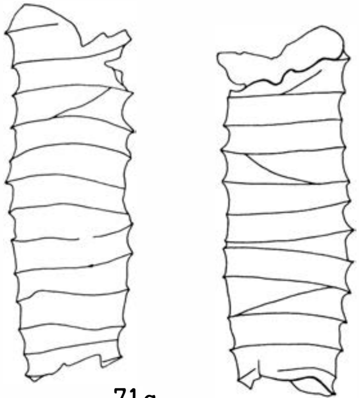


68

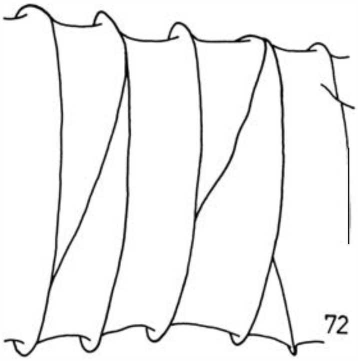


69


70


71a

71b


72

Figs. 68–72: ? Graptovermid gen. et sp. indet. (68) Two-layered wall structure. × 93. Hälludden horizon not known; Öl. 1237*c*. (69) Fine tubes preserved in wall of specimen. × 65. Hälludden – 100D; Öl. 1238*b*. (70) Close spacing of growth lines. × 65. Hagudden 0 – 8D; Öl. 1239*a*. (71) More widely spaced growth lines; (71*a*, *b*) two aspects. × 35. Hagudden 0 – 8D; Öl. 1239*b*. (72) Growth lines in detail. × 87. Hagudden 0 – 8D; Öl. 1240*d*.

structureless, possibly laminated layer (cf. the cortical layer), and an outer, fusellar layer; it is to be noted that, although two layers are developed as in the true graptolites, their relationship to one another is reversed in this case. It is possible to recover specimens in which only the structureless layer remains, and others with the walls composed only of the fusellar layer. In Öl. 1237*c* (Fig. 68), both layers are preserved, but the outer (fusellar) layer is partly ruckled over the inner (structureless) layer, which projects as a tube beyond the last growth band of the fusellar layer; this demonstrates the marked independence of the two layers. It should, perhaps, be emphasized that the inner layer has not been observed to act as secondary infilling tissue, it is clearly a part of the wall structure.

In Öl. 1238*b* (Fig. 69), two extremely fine tubes, about 0.015 mm in diameter, appear to be embedded in the wall of the specimen; these tubes clearly lie on the inner side of the fusellar layer, either between this and the structureless layer or within the substance of the latter. Their extent is not known: in one direction they become involved in the wrinkling and folding of the wall, and in the other, they run side by side to the broken edge of the specimen.

The number of fuselli developed in a given unit of length varies within the limits 9 to 38 per mm. The growth bands are not the half rings characteristic of almost all graptolites, but are complete rings beginning and ending at an oblique suture (Fig. 71 *a*, *b*). The growth lines between the fuselli take the form of prominent ridges, encircling the tubes in a collar-like fashion (Fig. 72); this feature is most pronounced where there are fewest growth bands per mm: compare Fig. 70 (32 per mm) with Fig. 72 (9 per mm).

DISCUSSION.—The material is provisionally attributed to the Graptovermida on the basis of the tubular form and the presence of fusellar structure, though it cannot be included in either of the genera placed therein. *Graptovermis* KOZŁOWSKI is an encrusting form, whilst the present material lacks any attachment surface. EISENACK (1936) has demonstrated fusellar structure in *Melanostrophus fokini* ÖPIK, 1930, but the periderm is of excessive thickness in this species and the growth bands are evident only after prolonged bleaching; the majority of the specimens recovered from the Ontikan limestones were yellow and transparent upon isolation (implying a slender periderm), requiring no subsequent treatment. It is of interest to note, however, that EISENACK described thickened, longitudinal strips in the walls of the tubes of *M. fokini* which he likened to the sicular virgella of the graptoloids; the fine tubes noted in Öl. 1238*b* (Fig. 69) could probably be interpreted as thicker bands in imperfectly cleared material. The tubes of *Melanostrophus* characteristically occur in complex associations, whereas those from the Ontikan limestones have only been recovered singly.

?*Melanostrophus* sp. BULMAN, 1944, differs from the present material in the indistinct definition of the growth lines and the presence of fusellar half rings, giving two zig-zag sutures.

The tuboid *Conitubus siculoides* KOZŁOWSKI has autothecae composed of fuselli in the form of complete rings, but in no instance does a specimen from the Ontikan limestones adopt the conical shape characteristic of the autothecae of this species.

In the stolothecae of the non-encrusting Stolonoidea, the fuselli are also complete rings; moreover, the part not occupied by the stolons is typically infilled with secondary tissue. The identity of the present material with the stolonoid structure is not complete, however: the walls are never perforated to enable the stolons to reach the exterior; tissue within the tubes seems to be restricted to the structureless inner layer of the walls; and the fine tubes preserved in Öl. 1238*b* can scarcely be reconciled with the prominent stolons characteristic of the Stolonoidea.

The resemblance of the present material to the free zooidal tubes of *Rhabdopleura normani* is worthy of note; the generally straight form of the tubes, the complete growth bands and the projecting, collar-like, growth lines are features common to both. This comparison is of particular interest in the light of KOZŁOWSKI's recent (1961) description of *Rhabdopleuroides expectatus* from Ordovician erratics; in this species, however, the zooidal tubes are encrusting (creeping) throughout their length.

Summary of Results

(1) A re-investigation of the syntypes of *Graptolithus bigsbyi* HALL, 1865, from Levis, Quebec, has revealed the presence of two species within the single species described by HALL; these are:

Tetragraptus bigsbyi (HALL, 1865)
Tetragraptus pseudobigsbyi sp. nov.

(2) An emended diagnosis of *Holmograptus* KOZŁOWSKI, 1954, is proposed: *Didymograptus cucullus* BULMAN, 1932, is excluded, while *Didymograptus lentus* TÖRNQUIST, 1911, *D. nodosus* HARRIS, 1926, and the several species of *Tylograptus* MU, 1957, are placed therein.

Didymograptus cucullus is selected as the type species of *Aulograptus* gen. nov.; *Didymograptus obscurus* EKSTRÖM, 1937, and *D. climacograptoides* BULMAN, 1931, are attributed to this genus.

The placement of *Holmograptus* and *Aulograptus* at the family level is discussed in JAANUSSON (1964).

(3) A revised diagnosis of *Maeandrograptus* MOBERG, 1892, is given emphasizing those characters which serve to distinguish this genus from *Isograptus* MOBERG, 1892. Three species are placed in *Maeandrograptus*:

Maeandrograptus schmalenseei MOBERG, 1892
Didymograptus leptograptoides MONSEN, 1937
Didymograptus mobergi TÖRNQUIST, 1901

and one species is attributed provisionally to the genus:

Maeandrograptus ? geniculatus sp. nov.

(4) *Atopograptus* HARRIS, 1926, and *Janograptus* TULLBERG, 1880, seem to be invalid genera, and *Atopograptus*, at least, can be regarded as a junior synonym of *Didymograptus* sensu lato. Both "genera" seem to have been established on stipe fragments which have undergone regeneration, thus accounting for their apparently sicula-less condition.

(5) The morphological characteristics of the Corynoididae are not sufficiently distinctive to merit the erection of either an order of the Graptolithina or

of a suborder of the Graptoloidea to accommodate this family. The balance of available evidence would seem to favour derivation from a dichograptid stock rather than directly from the Dendroidea.

(6) *Glyptograptus austrodentatus* var. *oelandicus* BULMAN, 1963, is given the status of subspecies.

Stratigraphical Conclusions

JAANUSSON (1960) has concisely summarised the problem attending the location of the *hirundo-bifidus* graptolite zonal boundary in Sweden: "the exact correlation of the beds in the boundary region between the zones of *D. hirundo* and *D. bifidus* is hampered by the circumstance that in Scandinavia nowhere the transition between these zones is developed as graptolitic shales. We do not know the details of the change in the graptolite faunas at this boundary" (p. 342).

The precisely located material which forms the subject of the present study does not completely resolve the question at issue, and the conclusions reached are that the zonal boundary in the section at Hälludden (Fig. 73) does not lie higher than +18 D, while at Hagudden it may lie at or below the disconformity (D). The evidence upon which these suggestions are based is presented below.

The opinion has been expressed by JAANUSSON (1960, pp. 341–342), and is favoured by the present writer (see above p. 43), that *Didymograptus callotheca* BULMAN, 1932, is a junior synonym of *Holmograptus lentus* (TÖRNQUIST, 1911). In Scandinavia, *H. lentus* would seem to be restricted to the Zone of *D. bifidus*. Thus, EKSTRÖM (1937) records the species from the Upper *Didymograptus* Shale immediately overlying the Komstad Limestone in the middle limestone quarry at Fågelsång, and *H. lentus* is there associated with *D. bifidus* and *Aulograptus obscurus* (EKSTRÖM, 1937). EKSTRÖM notes that *H. lentus* and *D. bifidus* do not range above the *bifidus* Zone in the shales, while *A. obscurus* extends just into the *murchisoni* Zone. Further, in the core of the Fågelsång boring, described by HEDE (1951), *H. lentus*, *D. bifidus* and *A. obscurus* are confined to the *bifidus* Zone. These species first appear in the Upper *Didymograptus* Shale some 20 cm above the upper surface of the Komstad Limestone. In fact, the Komstad Limestone has not yielded diagnostic graptoloids and the *hirundo-bifidus* zonal boundary may lie at the base, or at the top, or at any level within the limestone. Now, *Didymograptus callotheca* BULMAN is first recorded from Hälludden at the level +23 D (Fig. 73) and on the probability that this species is conspecific with *H. lentus* the *bifidus* Zone should be developed at least as low as +23 D.

BULMAN (1963, p. 675) has shown that *Glyptograptus dentatus* is probably confined to the *bifidus* Zone in Britain, and in the Hälludden section *G. dentatus* enters just below *H. lentus* at +18 D. This gives a probable lower limit to the *bifidus* Zone of +18 D, but it is not possible to deduce from the available evi-

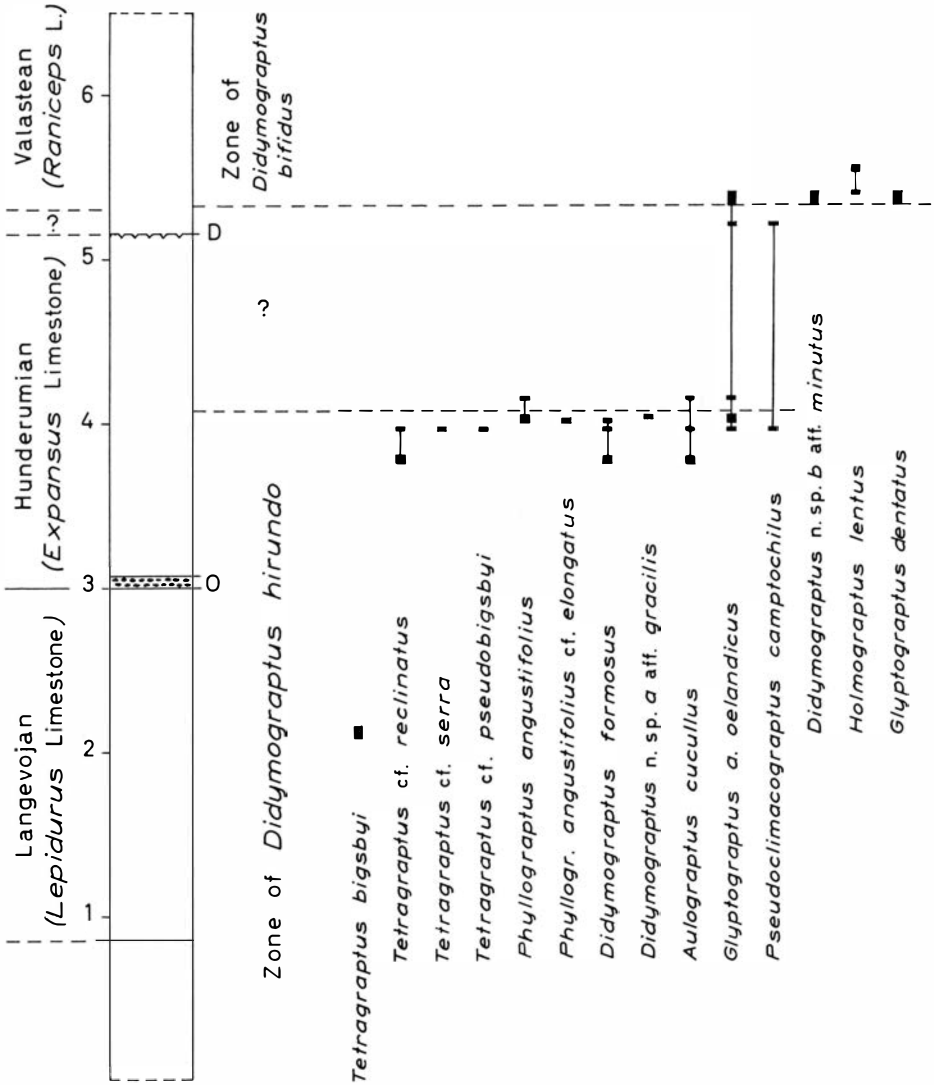


Fig. 73: Vertical distribution of graptoloids at Hälludden. *D:* discontinuity surface; *O:* oölitic limestone.

dence whether the *hirundo-bifidus* zonal boundary should be taken at +18 D or whether it lies at some distance below this level.

The evidence for the position of the zonal boundary at Hagudden is even more tentative, since the *bifidus* Zone indicator *H. lentus* has not been found at that locality. However, some significance can be attached to the entrance of *G. dentatus* between −8 D and the disconformity in view of the fact that, in Britain at least, this species appears to be confined to the *bifidus* Zone. Thus, it may be that the *bifidus* Zone in the Hagudden section is developed at least as low as D (or −8 D).

Table 3. A list of the graptoloids found at Hälludden and a tabular summary of their distribution.

Species	Levels from which collections made											
	−84 − 92	−135 − 140D	−118 − 120D	−113 − 116D	−110 − 113D	−100D	−76 − 82D	+5 + 8D	+10 + 30D	+18 + 22D	+23 + 26D	+38 + 43D
Tetragraptus bigsbyi	×											
Tetragraptus cf. *reclinatus*		×	×									
Tetragraptus cf. *serra*			×									
Tetragraptus cf. *pseudobigsbyi*			×									
Phyllograptus angustifolius				×	×	×						
Phyllograptus angustifolius cf. *elongatus*				×								
Didymograptus formosus		×	×	×								
Didymograptus n. sp. *a* aff. *gracilis*					×							
Didymograptus n. sp. *b* aff. *minutus*										×	×	
Holmograptus lentus											×	×
Aulograptus cucullus		×	×			×						
Dichograptid sp. *a*			×									
Dichograptid sp. *b*		×	×									
Dichograptid sp. *c*			×									
Dichograptid sp. *d*										×	×	
Glyptograptus austrodentatus oelandicus			×	×	×	×		×		×	×	
Glyptograptus dentatus										×	×	
Pseudoclimacograptus camptochilus			×					×				

It is not possible at present to effect an exact comparison of the data on the graptoloids given above with those units of the Ontikan limestone sequence which are based on shelly faunas (Dr. JAANUSSON *in litt.*, 1963). This derives not only from the uncertainties attending the delimitation of the graptolite zones but also from an incomplete knowledge of the shelly faunas themselves. To date, only the illaenids have been described (JAANUSSON, 1957) amongst the rich and varied shelly material from Öland, and the illaenids alone are not sufficient to define the exact limits of all the shelly faunal units. It is clear that the upper limit of the Langevoja Substage lies at the base of the oolitic bed (O—Fig. 73) at Hälludden, but the Hunderum–Valaste Substage junction may lie anywhere between the disconformity (D) and +15D. At Hagudden, the Langevoja Substage also ranges as high as the base of the oolitic bed, but for the present the Hunderum and Valaste Substages cannot be even tentatively delimited at this locality.

From the Hälludden section (Fig. 73), which is the more complete of the two, it is not possible to say more than that the lower part of the Hunderum

Table 4. A list of the graptoloids found at Hagudden and a tabular summary of their distribution.

Species	Levels from which collections made					
	−83−86	0−8 D	0+15 D	+10+15 D	+20+25 D	+20+45 D
Tetragraptus bigsbyi	×					
Didymograptus formosus		×				
Didymograptus cf. n. sp. *a* aff. *gracilis*			×	×		
Didymograptus n. sp. *b* aff. *minutus*		×	×			
Maeandrograptus? geniculatus	×					
Glyptograptus austrodentatus oelandicus						×
Glyptograptus dentatus			×	×		
Pseudoclimacograptus camptochilus			×			×

Substage probably lies high in the *hirundo* Zone and that the *hirundo–bifidus* boundary may coincide with the junction of the Hunderum and Valaste Substages or may lie within the upper part of the Hunderum Substage.

Evidence in favour of placing the graptolite boundary within the Hunderum Substage seems to be afforded by the sequence at Fågelsång, where the Komstad Limestone is underlain by shales of the *hirundo* Zone and overlain by shales of the *bifidus* Zone (EKSTRÖM, 1937). Unfortunately, this limestone in Scania is not, as yet, satisfactorily correlated with the succession in Öland, but in Dr. JAANUSSON's opinion "the main part of this formation [Komstad Limestone] is of Langevojan age (i.e. comparable to the zone of *Asaphus lepidurus*), but some species listed from this limestone indicate that in places the formation may include also beds comparable to the zone of *Asaphus expansus* [Hunderum Substage]" (1960, p. 345). Only if the whole of the Hunderum Substage is represented in the Komstad Limestone could the *hirundo–bifidus* zonal boundary coincide with that between the Hunderum and Valaste Substages.

The three divisions of the *Orthoceras* Limestone (3c) of the Oslo Region —the *Megalaspis* Limestone (3cα), the *Asaphus* Shale (3cβ) and the *Endoceras* Limestone (3cγ)—have been equated by JAANUSSON (1960, pp. 343–345) with the Langevoja, Hunderum and the greater part of the Valaste Substages, respectively, of the Ontikan shelly sequence. If the *hirundo–bifidus* zonal boundary is correctly drawn between the Hunderum and Valaste Substages it will lie between the *Asaphus* Shale and the *Endoceras* Limestone, but if the zonal boundary lies within the Hunderum Substage it will be found in the *Asaphus* Shale in Norway.

References

BERRY, W. B. N., 1960: Graptolite faunas of the Marathon region, West Texas. *Univ. Texas Public.*, No. 6005, pp. 1–179.

BOHLIN, B., 1949: The *Asaphus* Limestone in northernmost Öland. *Bull. Geol. Inst. Uppsala*, vol. 33, pp. 529–570.

BOHLIN, B. & JAANUSSON, V., 1955: The Lower Ordovician limestones between the *Ceratopyge* Shale and the *Platyurus* Limestone at Böda Hamn. *Ibidem*, vol. 35, pp. 111–173.

BOUČEK, B. & PŘIBYL, A., 1951: Taxonomy and phylogeny of some Ordovician graptolites. *Bull. Intern. Acad. Tchèq. des Sci.*, vol. 52, No. 1, pp. 267–283.

— 1953: On the genus *Diversograptus* MANCK from the Silurian of Bohemia. *Sborník Ústř. ústavu Geol.*, vol. 20, pp. 551–576.

BRONGNIART, A., 1828: *Historie des Végétaux Fossiles*, vol. 1, pp. 1–488, Paris.

BULMAN, O. M. B., 1931: South American graptolites with special reference to the Nordenskiöld Collection. *Arkiv för Zool.*, vol. 22 A, No. 3, pp. 1–111.

— 1932*a*: On the graptolites prepared by Holm. 1. Certain 'diprionidian' graptolites and their development. *Ibidem*, vol. 24A, No. 8, pp. 1–46.

— 1932*b*: Ditto 4. New species of *Didymograptus* and *Dicellograptus* from Öland, with remarks on the development of *Dicellograptus*. *Ibidem*, vol. 24A, No. 9, pp. 15–21.

— 1932*c*: Ditto 5. *Isograptus*, *Maeandrograptus* and the *Isograptus* mode of development. *Ibidem*, vol. 24A, No. 9, pp. 21–29.

— 1933: Notes on the evolution and morphology of certain Graptoloidea. *Ibidem*, vol. 24A, No. 13, pp. 1–37.

— 1936: On the graptolites prepared by Holm. 7. The graptolite fauna of the Lower *Orthoceras* Limestone of Hälludden, Öland, and its bearing on the evolution of the Lower Ordovician graptolites. *Ibidem*, vol. 28A, No. 17, pp. 1–107.

— 1938: Graptolithina. In SCHINDEWOLF, O. H., *Handb. der Paläozool.*, vol. 2D, Lief. 2, pp. 1–92. Berlin.

— 1944–47: Monograph of Caradoc (Balclatchie) graptolites from limestones in the Laggan Burn, Ayrshire. *Palaeontograph Soc.*, pp. 1–78. London.

— 1950*a*: Some didymograptids and associated forms from the *Phyllograptus* Shale of Tosåssen, Jämtland. *Geol. Fören. Förhandl.*, vol. 72, No. 4, pp. 389–396.

— 1950*b*: On some Ordovician graptolite assemblages of Belgium. *Bull. Inst. Roy. Sci. Nat. Belgique*, vol. 26, No. 5, pp. 1–8.

— 1953: Some graptolites from the *Ogygiocaris* Series of the Oslo district. *Arkiv för Min. och Geol.*, vol. 1, No. 17, pp. 509–518.

— 1955: Graptolithina with sections on Enteropneusta and Pterobranchia. *Treatise on Invert. Palaeo.*, pt. V, pp. 1–101. Lawrence, Kansas.

— 1958: The sequence of graptolite faunas. *Palaeontology*, vol. 1, pt. 3, pp. 159–173.

— 1963: On *Glyptograptus dentatus* (Brongniart) and some allied species. *Palaeontology*, vol. 6, pt. 4, pp. 665–689.

EISENACK, A., 1936: Was ist *Melanostrophus*? *Zeitschr. f. Geschiebeforsch.*, vol. 12, pp. 100–104.

EKSTRÖM, G., 1937: Upper *Didymograptus* Shale in Scania. *Sver. Geol. Unders.*, ser. C, No. 403, pp. 1–53.

ELLES, G. L., 1898: The graptolite fauna of the Skiddaw Slates. *Quart. Journ. Geol. Soc.*, vol. 54, pp. 463–549.

ELLES, G. L. & WOOD, E. M. R., 1901–18: Monograph of British graptolites. *Palaeontograph. Soc.*, pts. I–XI, pp. 1–539. London.

FRECH, F., 1897: Lethaea Geognostica, 1 Th. *Leth. Pal.*, vol. 1, No. 11, Graptolithen. Stuttgart.

GOTHAN, W., 1934: *Melanostrophus fokini* Öpik in einem untersilurischen Geschiebe der Stufe D1. *Diese Zeitschr.*, vol. 10, pp. 153–157. Leipzig.

HADDING, A., 1913: Undre *Dicellograptus*-skiffern i Skåne jämte några därmed ekvivalenta bildningar. *Lunds Univ. Årsskr.*, vol. 9, No. 15, pp. 1–91.

HALL, J. 1858: Description of Canadian graptolites. *Geol. Surv. Canada Rept. for 1857*, pp. 1–143. Montreal.

—— 1865: Graptolites of the Quebec Group. *Geol. Surv. Canada, Canadian Organic Remains*, dec. 2, pp. 1–151.

HALL, T. S., 1899: Graptolite-bearing rocks of Victoria, Australia. *Geol. Mag.*, vol. 36, pp. 438–451.

— 1914: Victorian graptolites, pt. IV. Some new or little known species. *Proc. Roy. Soc. Vict.*, *n.s.*, vol. 27, pp. 104–118.

HARRIS, W. J., 1916: The palaeontological sequence of the Lower Ordovician rocks of the Castlemain district, pt. 1. *Ibidem*, vol. 29, pp. 50–74.

— 1924: Victorian graptolites, new series, pt. I. *Ibidem*, vol. 36, pp. 92–106.

— 1926: Victorian graptolites, new series, pt. II. *Ibidem*, vol. 38, pp. 55–61.

— 1933: *Isograptus caduceus* and its allies in Victoria. *Ibidem*, vol. 46, pp. 79–114.

HARRIS, W. J. & KEBLE, R. A., 1932: Victorian graptolite zones with correlation and description of species. *Ibidem*, vol. 44, pp. 25–48.

HARRIS, W. J. & THOMAS, D. E., 1935: Victorian graptolites, new series, pt. III. *Ibidem*, vol. 47, pp. 288–313.

HEDE, J. E., 1951: Boring through Middle Ordovician–Upper Cambrian in the Fågelsång district, Scania (Sweden). *Lunds Univ. Årsskr.*, vol. 46, avd. 2, No. 7, pp. 5–84.

HOLM, G., 1890: Gotlands Graptoliter. *Bihang till K. Svenska Vet.-Akad. Handl.*, vol. 16, avd. 4, No. 7, pp. 1–34.

— 1895: Om *Didymograptus*, *Tetragraptus* och *Phyllograptus*. *Geol. Fören. Förhandl.*, vol. 17, pp. 319–359. (Eng. trans. by ELLES, G. L. & WOOD, E. M. R., 1895, *Geol. Mag.*, vol. 32, pp. 433–492).

HOPKINSON, J., 1872: On the occurrence of a remarkable group of graptolites in the Arenig rocks of St. David's, S. Wales. *Geol. Mag.*, vol. 9, p. 467.

HOPKINSON, J. & LAPWORTH, C., 1875: Descriptions of the graptolites of the Arenig and Llandeilo rocks of St. David's. *Quart. Journ. Geol. Soc. London*, vol. 31, pp. 631–673.

HSÜ, S. C., 1934: The graptolites of the Lower Yangtze Valley. *Mon. Acad. Sinica, Nat. Res. Inst. Geol.*, ser. A, vol. 4, pp. 1–106.

— 1959: A new graptolite fauna from the Lower Ordovician Shale of Tsaidam, Chinghai Province. *Acta Pal. Sinica*, vol. 7, pp. 176–191.

JAANUSSON, V., 1957: Unterordovizische Illaeniden aus Skandinavien. *Bull. Geol. Inst. Uppsala*, vol. 37, pp. 79–165.

— 1960: Graptoloids from the Ontikan and Viruan (Ordov.) limestones of Estonia and Sweden. *Ibidem*, vol. 38, pp. 290–366.

— 1964: Two multiramous graptoloids from the Lower Didymograptus Shale of Scandinavia. *Geol. Fören. Förhandl.*, vol. 86, No. 4, pp. 413–432.

KOZŁOWSKI, R., 1953: Badania nad nowym gatunkiem z rodzaju *Corynoides* (Graptolithina). *Acta Geol. Polonica*, vol. 3, pt. 2, pp. 193–209.

— 1954: Sur la structure de certains Dichograptidae. *Ibidem*, vol. 4, pt. 4, pp. 423–444.

— 1956: Nouvelles observations sur les Corynoididae (Graptolithina). *Acta Pal. Polonica*, vol. 1, No. 4, pp. 259–269.

— 1961: Découverte d'un Rhabdopleuridé (Pterobranchia) ordovicien. *Ibidem,* vol. 6, pt. 1, pp. 3–16.

KRAFT, P., 1926: Ontogenetische Entwicklung und Biologie von *Diplograptus* und *Monograptus*. *Pal. Zeitschrift,* vol. 7, pp. 207–249.

LAPWORTH, C., 1873: On an improved classification of the Rhabdophora. *Geol. Mag.,* vol. 10, pp. 500–504, 555–560.

— 1879–80: On the geological distribution of the Rhabdophora. *Ann. Mag. Nat. Hist.,* ser. 5, vol. 3, pp. 245–257, 449–455; vol. 4, pp. 333–341; vol. 5, pp. 273–285; vol. 6, pp. 16–29, 185–207.

MOBERG, J. C., 1891: Om ett par synonymier. *Geol. Fören. Förhandl.,* vol. 13, avd. 3, No. 136, pp. 216–222.

— 1892: Om några nya graptoliter från Skånes Undre Graptolitskiffer. *Ibidem,* vol. 14, avd. 4, No. 144, pp. 339–349.

MONSEN, A., 1937: Die Graptolithenfauna im Unteren *Didymograptus*-schiefer (*Phyllograptus*-schiefer) Norwegens. *Norsk Geol. Tidsskrift,* vol. 16, pp. 57–266.

MU, A. T., 1957: Some new or little known graptolites from the Ningkuo Shale (Lower Ordovician) of Changshan, western Chekiang. *Acta Pal. Sinica,* vol. 5, No. 3, pp. 369–438.

MU, A. T. & LEE, C. K., 1958: Scandent graptolites from the Ningkuo Shale of the Kiangshan–Changshan area, western Chekiang. *Ibidem,* vol. 6, pt. 4, pp. 391–427.

MULDNER, A., 1934: Über untersilurische Geschiebe der Stufe D1. *Zeitschr. Geschiebeforschung,* vol. 10, pp. 151–152. Leipzig.

NICHOLSON, H. A., 1868: On the graptolites of the Skiddaw Series. *Quart. Journ. Geol. Soc.,* vol. 24, p. 140.

— 1875: On a new genus and some new species of graptolites from the Skiddaw Slates. *Ann. Mag. Nat. Hist.,* vol. 16, pp. 269–273.

NICHOLSON, H. A. & MARR, J. E., 1895: Notes on the phylogeny of the graptolites. *Geol. Mag.,* vol. 32, pp. 529–539.

ÖPIK, A., 1930: Beiträge zur Kenntnis der Kukruse (C2–C3) Stufe in Eesti. IV. *Acta et Comm. Univ. Tartuensis (Dorpat.),* vol. A19, pt. 2, pp. 1–34.

PŘIBYL, A., 1947: Classification of the genus *Climacograptus*. *Bull. Intern. Acad. Tchèq. Sci.,* vol. 58, pt. 2, pp. 1–12.

RIGBY, J. K., 1958: Lower Ordovician graptolite faunas of western Utah. *Journ. Pal.,* vol. 32, No. 5, pp. 907–917.

RUEDEMANN, R., 1904–08: Graptolites of New York, pts. I & II. *New York State Mus. Mem.,* No. 7, pp. 457–803; No. 11, pp. 4–583.

— 1947: Graptolites of North America. *Geol. Soc. Am. Mem.,* No. 19.

SKEVINGTON, D., 1963: Graptolites from the Ontikan Limestones (Ordovician) of Öland, Sweden. I. Dendroidea, Tuboidea, Camaroidea and Stolonoidea. *Bull. Geol. Inst. Uppsala,* vol. 42, pp. 1–62.

SPJELDNÆS, N., 1953: The Middle Ordovician of the Oslo Region, 3. Graptolites dating the beds below the Middle Ordovician. *Norsk Geol. Tidsskr.,* vol. 31, pp. 171–184.

STØRMER, L., 1953: The Middle Ordovician of the Oslo Region. 1. Introduction to stratigraphy. *Norsk Geol. Tidsskr.,* vol. 31, pp. 37–141.

STRACHAN, I., 1949: On the genus *Corynoides* Nicholson. *Geol. Mag.,* vol. 86, pp. 153–160.

— 1952: On the development of *Diversograptus* Manck. *Ibidem,* vol. 89, pp. 365–368.

— 1959: Graptolites from the *Ludibundus* Beds (Middle Ordovician) of Tvären, Sweden. *Bull. Geol. Inst. Uppsala,* vol. 38, pp. 47–68.

STUBBLEFIELD, C. J., 1929: Notes on some early British graptolites. *Geol. Mag.,* vol. 66, pp. 268–285.

THOMAS, D. E., 1960: The zonal distribution of Australian graptolites. *Journ. Proc. Roy. Soc. N.S.W.*, vol. 94, pp. 1–58.

THORSTEINSSON, R., 1955: The mode of cladial generation in *Cyrtograptus*. *Geol. Mag.*, vol. 92, pp. 37–49.

TJERNVIK, T. E., 1956: On the early Ordovician of Sweden. Stratigraphy and fauna. *Bull. Geol. Inst. Upps.*, vol. 36, pp. 107–284.

— 1960: The Lower *Didymograptus* Shale of the Flagabro drilling core. *Geol. Fören. Förhandl.*, vol. 82, h. 2, pp. 203–217.

TÖRNQUIST, S. L., 1879: Några iakttagelser öfver Dalarnes graptolitskiffrar. *Geol. Fören. Förhandl.*, vol. 4, pp. 446–457.

— 1883: Öfversigt öfver bergbyggnaden inom Siljansområdet i Dalarne, med hänsyn företrädesvis fäst vid dess paleozoiska lag. *Sver. Geol. Unders.*, ser. C, No. 57, pp. 1–59.

— 1890–92: Undersökningar öfver Siljansområdets graptoliter, pts. I & II. *Lunds Univ. Årsskr.*, vol. 26, pp. 1–33; vol. 28, pp. 1–47.

— 1893: Observations on the structure of some Diprionidae. *Ibidem*, vol. 29, pp. 1–14.

— 1901–04: Graptolites of the lower zones of the Scanian Vestrogothian *Phyllo-Tetragraptus* Beds, pts. I & II. *Ibidem*, vol. 37, pp. 1–26; vol. 40, pp. 1–29.

— 1911: Graptolitologiska bidrag 3–7. *Geol. Fören. Förhandl.*, vol. 33, pp. 421–438. Stockholm.

TULLBERG, S. A., 1880*a*: Några *Didymograptus*-arter i undre graptolitskiffer vid Kiviks-Esperöd. *Ibidem*, vol. 5, pp. 39–43.

—— 1880*b*: Tvenne nya graptolitslägten. *Ibidem*, vol. 5, pp. 313–315.

— 1882–3; Skånes graptoliter, I & II. *Sver. Geol. Unders.*, ser. C, No. 50, pp. 1–44.

URBANEK, A., 1963: On generation and regeneration of cladia in some Upper Silurian monograptids. *Acta Pal. Polonica*, vol. 8, No. 2, pp. 135–254.

WALKER, M., 1953: The development of a diplograptid from the Platteville Limestone. *Geol. Mag.*, vol. 90, pp. 1–16.

WIMAN, C., 1894*a*: Ueber Diplograptidae Lapworth. *Bull. Geol. Inst. Uppsala*, vol. 1, pp. 97–104.

— 1894*b*: Ueber die Silurformation in Jemtland. *Ibidem*, pp. 256–276.

— 1895: Ueber die Graptolithen. *Ibidem*, vol. 2, pp. 239–316.

Tryckt den 27 oktober 1965.